BOTANICAL GAZETTE

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THE BOTANICAL GAZETTE

EDITOR

JOHN MERLE COULTER

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ERRATA

P. 31, second paragraph, line 4, for 500 read 5000.
P. 126, line 5 from bottom, for $\rho = 0.500$ read $r = 0.500$.
P. 214, line 7 from bottom, for b' read b.
P. 220, line 7, for pod read pad.
P. 222, line 22, for Linneaus' read Linnaeus'.
P. 300, line 10 from bottom, for *S. glaubescens* read *S. glaucescens*.
P. 300, last line, for (fig. 8) read (fig. 6).
P. 318, line 11, for represent read represents.
P. 355, line 17, for dropper read runner.
P. 382, line 2, for *Alpanes* read *Aplanes*.

Vol. L No. 1

THE BOTANICAL GAZETTE

July 1910

Editor: JOHN M. COULTER

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VOLUME L NUMBER 1

BOTANICAL GAZETTE

JULY 1910

RATIO OF PHOSPHATE, NITRATE, AND POTASSIUM ON ABSORPTION AND GROWTH[1]

OSWALD SCHREINER AND J. J. SKINNER

(WITH NINE FIGURES)

In this paper are reported the results of experiments obtained in connection with a study of the effects of harmful soil constituents upon plant growth and upon soil solutions and fertilizer action. The results here reported are especially with reference to the growth made by wheat seedlings in culture solutions containing many different ratios of phosphate, nitrate, and potash, and in regard to the ratio of these constituents originally present and removed by the wheat seedlings in the course of the experiment. In these investigations solution cultures containing the three fertilizer ingredients, namely P_2O_5, NH_3, and K_2O, as calcium acid phosphate, sodium nitrate, and potassium sulfate, respectively, in all possible ratios of one, two, and three constituents, varying them in stages of 10 per cent, were prepared, the concentration being 80 parts per million in these constituents. The selection of the salts as carriers of phosphate, nitrate, and potash, and the statement of the results in terms of P_2O_5, NH_3, and K_2O, are in harmony with the practice in fertilizer work and, for the sake of simplicity, these designations are also retained in the present paper. The salts selected, it will be seen, are also carriers of calcium, of sodium, and of sulfate, and the three salts, therefore, are the best that could be selected for giving at the same time other needed constituents.

The culture solutions of these three salts contained in each case a total concentration of 80 parts per million of P_2O_5, NH_3, and K_2O,

[1] Published by permission of the Secretary of Agriculture.

but these varied, as above noted, in the ratio in which they were present. Wheat plants were grown in these various cultures and observations were made in regard to general development, the effect on root growth, and appearance. The green weight of the plants was taken at the termination of the experiment. The solutions were changed every three days and an analysis made, the phosphate, nitrate, and potash being determined, thus giving the concentration of these constituents and the ratio existing at the end of every three-day period for comparison with the original concentration and ratio. This changing of the solutions was kept up for twenty-four days, thus making eight changes. In this work the methods[2] devised in these laboratories for the determination of small amounts of such constituents rendered excellent service and point a way for their further use upon other problems in connection with the biochemical relationships of soils and plants, which have hitherto been impossible of attack. In the discussion and presentation of the results, the triangular diagram as used in physical chemistry was employed, and has proven very useful as a guide in the work for the systematic handling of the experimental details. The results can best be presented and interpreted by its means, and the method should prove very useful as a guide in other lines of experimental work where similar relationships are involved.

The use of the triangular diagram as a guide in the work

The number of solution cultures required in order to have all the possible ratios as outlined above is sixty-six. To bear in mind these ratios for three different ingredients, together with the ratios of the solutions after the plants had grown, and perhaps also the ratios of the material removed from the solution, a total of 594 numbers, is practically an impossibility, and it is readily seen that in order to discuss such a comprehensive experiment as this the material must be reduced to a workable basis, so that the various phases of the results can be kept in mind and the proper correlation and comparisons made. The triangular diagram as suggested by SCHREINE-

[2] SCHREINER, O., and FAILYER, G. H., Colorimetric, turbidity, and titration methods used in soil investigations. Bulletin 31, Bureau of Soils, U.S. Dept. Agric. 1906.

MACHER[3] in 1893 and again by BANCROFT[4] in 1902 has been of the greatest service to physical chemistry, where both theoretical and practical consideration of percentage composition of three component parts are concerned.

In the present investigation we have likewise to consider the three component parts of the fertilizer mixture; namely P_2O_5, NH_3, and

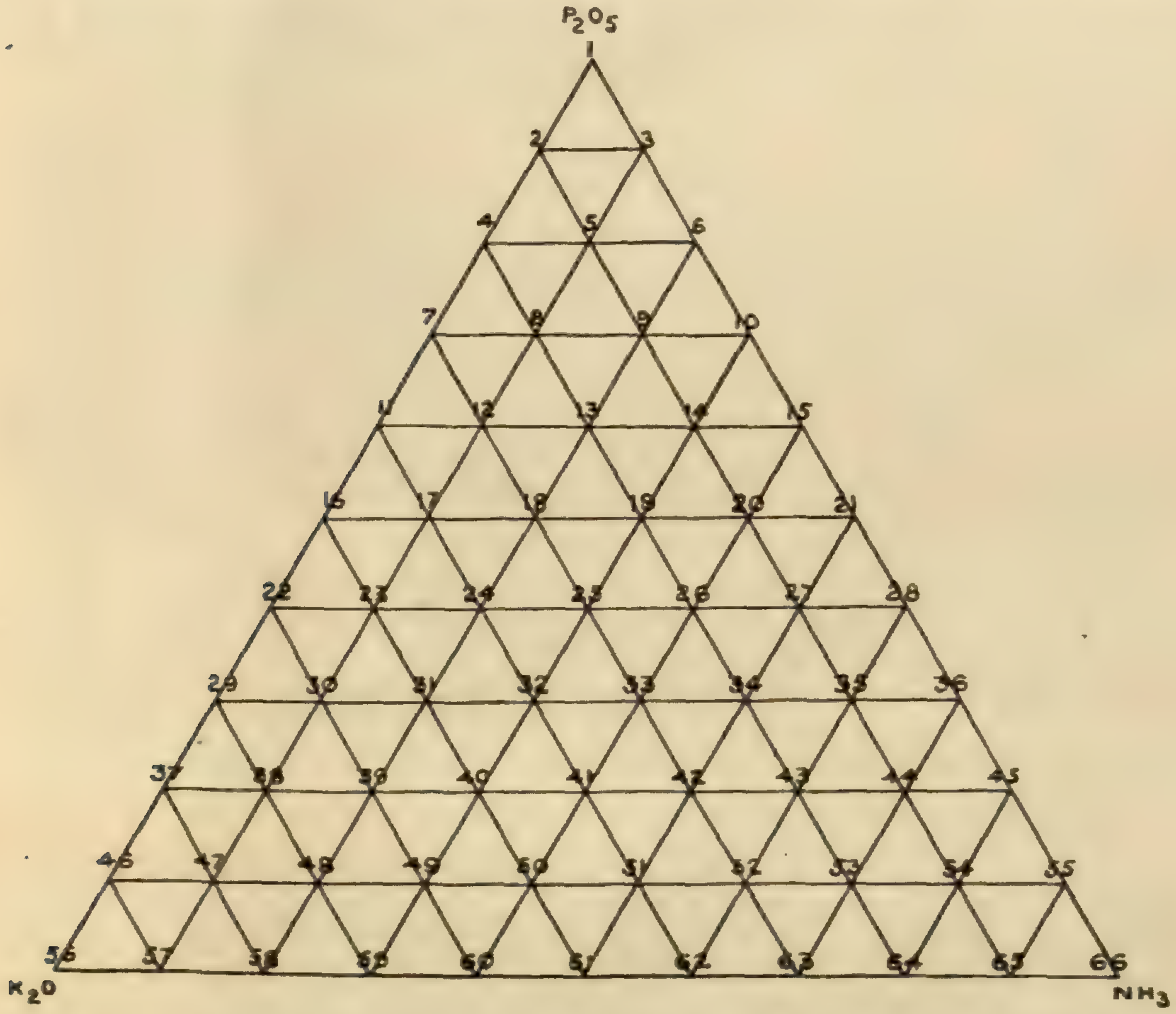

FIG. 1.—Showing the triangular diagram, with the points numbered, which represent the 66 culture solutions.

K_2O. It is possible, therefore, to represent any mixture of these three component parts in the triangular diagram. Such a triangular diagram is shown in fig. 1. It is an equilateral triangle in which the extreme points of the angles represent 100 per cent respectively of

[3] SCHREINEMACHER, F. A. H., Konzentrierung oder Verdünnung einer Lösung bei Konstanter Temperatur. Zeit. Phys. Chem. **11**:81. 1893.

[4] BANCROFT, W. D., Synthetic analysis of solid phases. Jour. Phys. Chem. **6**:178. 1902.

each of the ingredients, P_2O_5, NH_3, and K_2O, as shown in the diagram. Each side of the triangle is divided into ten equal parts, and lines are drawn connecting these points.[5] In the diagram, for the sake of ready reference, the intersections of these lines have been numbered. If we consider the line representing the base of the triangle, it is obvious that the point which represents 100 per cent K_2O (number 56 in the diagram) represents at the same time 0 per cent NH_3, and the point 100 per cent NH_3 (number 66) likewise represents 0 per cent K_2O. If we take a point half-way between these two points, for instance point 61, we have a mixture of the two salts in equal proportions; i.e., the fertilizer constituents represented by that point will be 50 per cent K_2O and 50 per cent NH_3. Similarly, point 16 represents 50 per cent K_2O and 50 per cent P_2O_5, and point 21 represents 50 per cent NH_3 and 50 per cent P_2O_5. If we take a point nearer to either of the corners, we will have a higher percentage of that ingredient and a correspondingly lower percentage of the other. For instance, at the point 59 the composition is 70 per cent K_2O and 30 per cent NH_3; at 29 it is likewise 70 per cent K_2O, but 30 per cent P_2O_5; at 64 it is 20 per cent K_2O and 80 per cent NH_3; at 45 it is likewise 80 per cent NH_3, but 20 per cent P_2O_5.

As stated above, points on the base line 56 to 66 represent mixtures containing no P_2O_5. The next line above this, namely 46 to 55, represents mixtures containing throughout 10 per cent P_2O_5, but varying amounts of the other two constituents. Similarly, the line 37 to 45 represents throughout 20 per cent mixtures of P_2O_5; line 29 to 36, 30 per cent mixtures of P_2O_5; and so on upward until point 1, the apex of the triangle, is reached, where the composition is 100 per cent P_2O_5, as already explained. Similarly, points on the line 1 to 66 represent 0 per cent K_2O; line 2 to 65 represents 10 per cent K_2O, but varying amounts of P_2O_5 and NH_3; and so on until at point 56 the composition is 100 per cent K_2O. Likewise, points on the line 1 to 56 represent 0 per cent NH_3; line 3 to 57 represents 10 per cent NH_3, but varying amounts of P_2O_5 and K_2O; and so on until at point 66 the composition is 100 per cent NH_3. It is obvious,

[5] Such diagrams for physical chemical work, giving still finer rulings, namely 100 to each line, can be purchased from the Cornell Co-operative Society, and were used in these investigations.

therefore, that any point within the triangle represents a mixture composed of the three constituents, its position in the triangle being determined by the composition of the mixture, namely the ratio of the three component parts, P_2O_5, NH_3, and K_2O. For instance, point 12, being on the 60 per cent phosphate line, represents this composition of P_2O_5, namely 60 per cent, and being at the same time on the 10 per cent NH_3 line, and the 30 per cent K_2O line, it represents 10 per cent and 30 per cent of these constituents, respectively. The composition of the mixture represented by this point is, therefore, P_2O_5 60 per cent, NH_3 10 per cent, K_2O 30 per cent; i.e., the ratio of these constituents in the fertilizer mixture is 60–10–30 or 6–1–3. Similarly, the point 34 represents the following mixture of the composition: P_2O_5 30 per cent, NH_3 50 per cent, K_2O 20 per cent, or a fertilizer ratio of 3–5–2.

For the sake of convenience in stating such ratios or percentage composition of the fertilizer mixtures in this investigation, the figures are always given in the order P_2O_5, NH_3, and K_2O, as shown above.

The triangle, therefore, represents single fertilizer constituents at the apices or vertices, mixtures of any two constituents along the boundary lines of the triangle, and mixtures of all three constituents within the triangle.

Solution culture methods

Before proceeding with a description of the general appearance of the cultures growing in solutions with the different fertilizer ratios, it may be well to describe briefly here the solution-culture method used in these experiments, as the manner of procuring a sufficiently large number of seedlings and of preparing physiologically pure water are important factors in carrying on this or allied investigations.

METHOD OF PROCURING UNIFORM SEEDLINGS

In the work under consideration, as well as in other work in progress in these laboratories, it is necessary to have a large number, often several hundred and sometimes thousands, of uniform seedlings; i.e., seedlings of the same age and equal in development and general vitality. The general principle on which this equal germination of

wheat seedlings is based has already been described by LIVINGSTON[6] and in former bulletins of this bureau.[7] The method consists in having a perforated disk, supported by ordinary corks in such a way that it will just float upon the surface of a pan of water. In the earlier work a wire gauze, which had been coated with paraffin so as to make virtually a plate of paraffin reinforced by wire, was used, holes being made in this plate by means of a hot wire. Perforated cork sheets, preferably paraffined, have also been used. In this case sheet cork about one-eighth of an inch in thickness is immersed in melted paraffin, and after removal from the paraffin this is allowed to harden in the air spaces of the cork. Holes are then made by means of a small cork borer so as to give a perforated plate. Both of these plates are open to objections. In the paraffined plate, when it is used continually, there is a tendency for the paraffin to split off from the wire, which is thus exposed to the action of the water and the roots; moreover, this plate is not easily repaired. The cork plate, on the other hand, shows considerable tendency to warp, is rather fragile, and is not easily kept sterile.

Instead of these plates there were used in these present experiments perforated hard-rubber sheets, thus overcoming the above objections to a considerable degree. These are prepared by cutting a circular disk of 305 mm. from vulcanized sheet rubber 3.2 mm. in thickness. By clamping several of these tightly together, preferably between layers of wood, small holes are drilled through the mass approximately 4.8 mm. in diameter and 5.0 mm. apart. Disks of this material float level upon the water when supported by corks, are not so subject to warping, and are readily cleaned and kept sterile. The corks are fastened to the under surface of the disk in four or five places on the circumference and in the center. For this purpose either rubber or wooden pegs or wire may be used; if the latter, it should be made either of iron or aluminum, never of brass or copper. The size of the corks is so gauged by trial that the disk is just supported on the surface

[6] LIVINGSTON, B. E., A simple method for experimenting with water cultures. Plant World **9**:13. 1906.

[7] SCHREINER, O., and REED, H. S., Some factors influencing soil fertility. Bulletin 40, Bureau of Soils, U.S. Dept. Agric. 1907.

of the water. After floating this perforated disk on the surface of the water, the wheat seed, which has been previously soaked for about two hours, not longer, is spread evenly over the surface. This method insures an even germination of the seed and has the advantage of keeping the seed and later the young seedlings just moist. The seeds are never submerged in the water, nor do they remain suspended dry above the water. The roots grow through the holes of the disk into the liquid below. This method of sprouting wheat seedlings is far superior to growing them in sand, since the seedlings are more uniform and the apparatus can be kept sterile much more readily than sand. Furthermore, for water culture purposes the seedling is readily removed by merely lifting it from the disk. In this way the roots or delicate root hairs suffer no injury whatever, while in removing seedlings from sand some injury would be unavoidable. Moreover, the seedlings are removed direct from water to grow in solutions, and thus have the advantage of germinating in a medium similar to that in which they are to be grown.

The water in the germinating pans may be distilled water, if desired, or where good tap water can be secured this may be used. The water in the pans is changed daily, or, during the warm weather, twice a day. Several hundred uniform seedlings can be procured from a single disk of the kind described. Whatever inferior plants occur are rejected. For the bottle culture work described in this bulletin, the seedlings were used when the plumule was about 2 cm. high and just ready to emerge from the enveloping sheet.

More recently disks of perforated aluminum have been used in this laboratory and have proven very satisfactory. These disks are floated by means of a raft of sealed glass tubing of such dimensions as is required to float the plates in the manner above described. Three lengths of tubing 102 cm. long, 35 mm. in diameter, with approximately a 1.5 mm. wall thickness, were sufficient to float six aluminum disks 30 cm. in diameter and 1.6 mm. in thickness. The lengths of sealed tubing and two glass rods 56 cm. long and 12 mm. in diameter are wired together into a raft. The entire arrangement is floated in a porcelain-lined iron tank. Fig. 2 shows this tank with seedlings at various stages of development.

NOTCHING CORKS AND MOUNTING SEEDLINGS

The bottles used in these cultures are made of flint glass, have a capacity of about 250 cc., a total height of 100 mm., an outside diameter of 70 mm. at the bottom, a neck about 20 mm. high, and a mouth 57 mm. in diameter. This bottle is stoppered by means of a soft, flat cork about 12 mm. in thickness and notched for holding the seedlings. The method of notching these corks consists in cutting ten vertical, triangular wedges from the circumference. Each wedge after being cut out is truncated, so that when replaced a small triangular opening, through which the plumule of the seedling will pass,

FIG. 2.—Method of germinating wheat seedlings on aluminum disks, which are floated in an enameled tank; disk to right elevated to show the plant roots.

is formed. This hole should be large enough to hold the seedling firmly and yet not bruise or injure it in any way by pressure. Around the circumference of the cork and in the upper half a groove is made sufficiently large to hold a small rubber band. After the wedges are inserted, the band keeps them in place and allows the cork with the seedlings to be handled readily and put into or taken out of the bottle without disturbing the plants. The seedlings are most easily inserted in the cork in the following manner: The cork with the ten wedges held in place by the rubber band is taken in the left hand and the seedling in the right hand. The plumule is pushed through the small, triangular opening, and then pulled up until the seed is close against the cork. When older seedlings, in which the leaves have unfolded

themselves, are to be used for an experiment, or where plants such as cowpeas are used, the wedge must be removed, the seedling put in place, and the wedge and rubber band replaced.

PREPARATION OF PHYSIOLOGICALLY PURE WATER

It is safe to say that ordinary distilled water, such as is commonly found in laboratories, is unsuited for culture experiments. This is due to a variety of causes which need not be entered into here, but which are discussed in a bulletin by LIVINGSTON.[8] Such water, while pure from a chemical and physical standpoint, is nevertheless not suited for such delicate indicators as plants, which are highly susceptible even to very minute quantities of toxic materials. Such water can be improved by distillation with strong oxidizing agents, such as potassium permanganate in alkaline solution or potassium bichromate in acid solution. The far simpler method already described by LIVINGSTON[8] has given very satisfactory results in this laboratory. In this method the water is purified by shaking it with a highly absorptive carbon black, which removes from the water any traces of injurious bodies it may contain. Not all carbon black possesses this property to an equal degree; the variety used in this laboratory is known as the "G Elf" brand, and is prepared on a commercial scale by burning natural gas and condensing the finely divided carbon on cooled surfaces. It is the same carbon black used for the purpose of decolorizing soil and plant solutions in this laboratory. For the present purpose the carbon black is thoroughly washed with distilled water as an added precaution, although it is not definitely known whether anything is thereby removed from it or not. The carbon black is then kept in this moist condition mixed with water so as to form a thin paste. About 10 cc. of this paste is added to each liter of water which is to be purified, and after shaking the mixture is allowed to stand for fifteen to thirty minutes and then filtered through an ordinary filter paper into a clean, hard-glass receptacle. Water treated thus is very satisfactory for the growth of plants in solution cultures.

[8] LIVINGSTON, B. E., Further studies on the properties of unproductive soils. Bulletin 36, Bureau of Soils, U.S. Dept. Agric. 1907.

General behavior of the cultures containing different fertilizer ratios

The plants in the different cultures prepared as described in the previous section show some marked differences almost from the very outset. After several changes of solution have been made, these differences become quite prominent. The most marked of these is

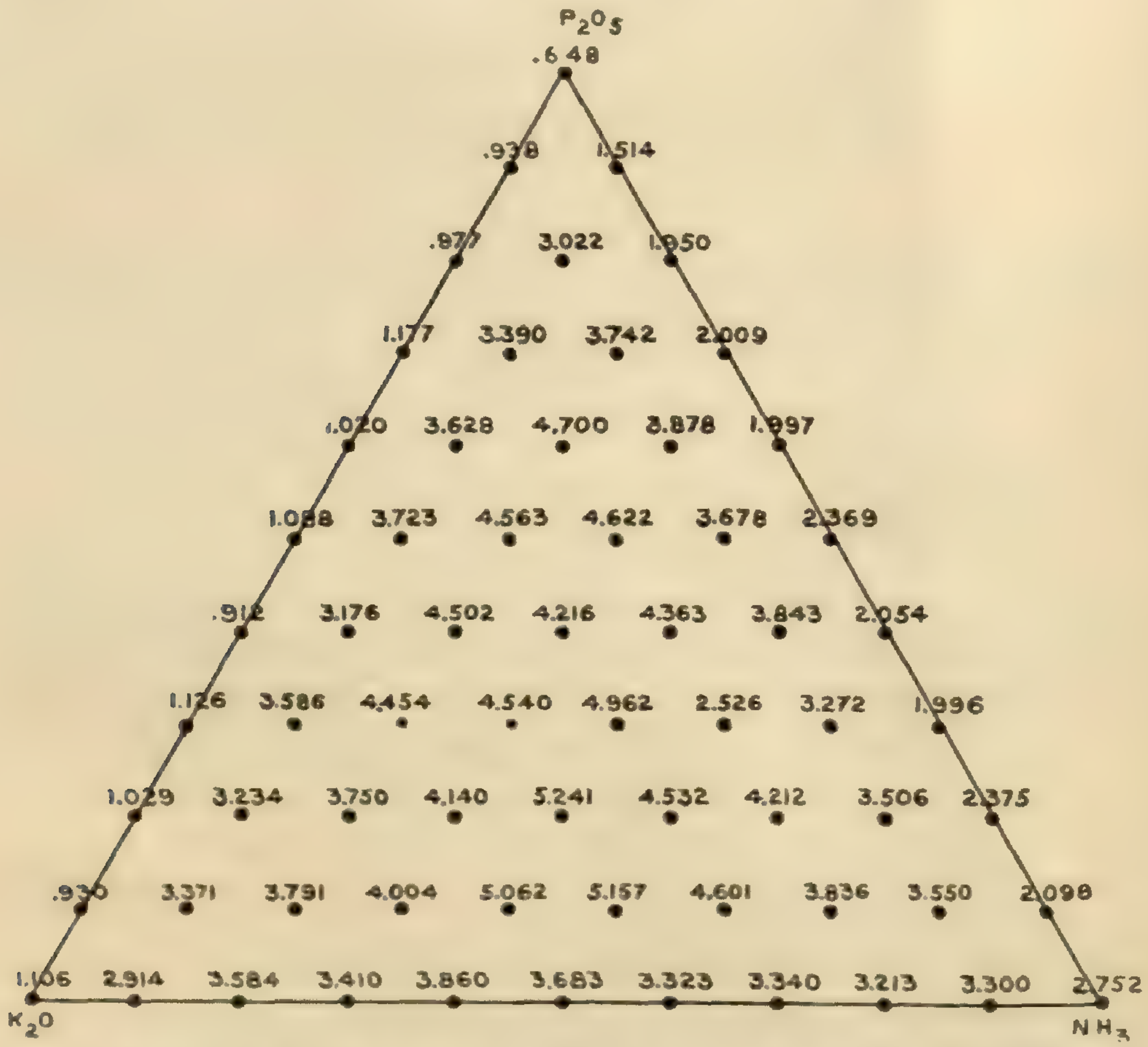

FIG. 3.—Green weight of 10 wheat plants grown in 66 cultures with different ratios of P_2O_5, NH_3, and K_2O.

that the solutions containing only one or two of the fertilizer ingredients, i.e., the entire periphery of the triangle, show a markedly less development of the plants than the cultures in the interior of the triangle wherein the three elements are combined. In other words, even the addition of only 10 per cent of the third element to mixtures of the other two produces a very appreciable increase in plant growth. This effect is most noticeable in the change from no nitrate to 10 per

cent nitrate. Of the single fertilizer ingredients, the nitrate culture is the best, and this is usually followed by the potassium culture, the phosphate culture being in general the poorest of the entire triangle. The cultures in the interior of the triangle do not show so marked a difference, although it is apparent that there is a tendency toward a rise in the middle of any line, this being displaced somewhat along some of the lines so as to give the effect of the highest and better region of growth lying in the middle of the lower part of the triangle; i.e., nearer to the potassium-nitrogen base. The set grew from February 25 to March 21. The green weights obtained in the sixty-six cultures are given in the triangular diagram shown in fig. 3. A more detailed discussion as well as grouping of these green weights, their correlation with the concentration of the solution, and the amount of nutrients removed will be given later.

As has already been stated, the solutions were analyzed every third day for the three component fertilizer parts, phosphate, nitrate, and potash, expressed as P_2O_5, NH_3, and K_2O. The original concentrations in these elements were in the sum total 80 parts per million. After the analysis the sum total of the three component parts was again calculated and the average concentrations of these three elements was again ascertained for the eight periods. The average concentrations will be found in the diagram in fig. 4. It is thus apparent that more of the essential ingredients were removed in the interior of the triangle; i.e., there was a greater absorption where all three were combined than where only two elements were present, and the least removal took place in those cultures where the single salts were present. It is also noticeable that in the solutions containing the three fertilizer elements the greatest removal occurred in that region of the diagram where the greatest growth occurred. A more detailed discussion of these results and their component parts will be given later in this paper.

Ratios of P_2O_5, NH_3, and K_2O, found in the various cultures

It might be said that in all cases the ratio in the final solution was never the same as the original ratio. The amount of change which had taken place, however, was markedly different in the different solutions and depended largely upon what the original ratio was. In

order to show this change in ratio of the fertilizer ingredients, the triangular diagram is of the greatest service, for without this it would be impossible to get an intelligent idea of what had occurred in the solution. In the diagram fig. 5 are given the original ratios of the fertilizer constituents, the ratios left in these solutions as shown by analysis, and the corresponding ratio of the removed constituents.

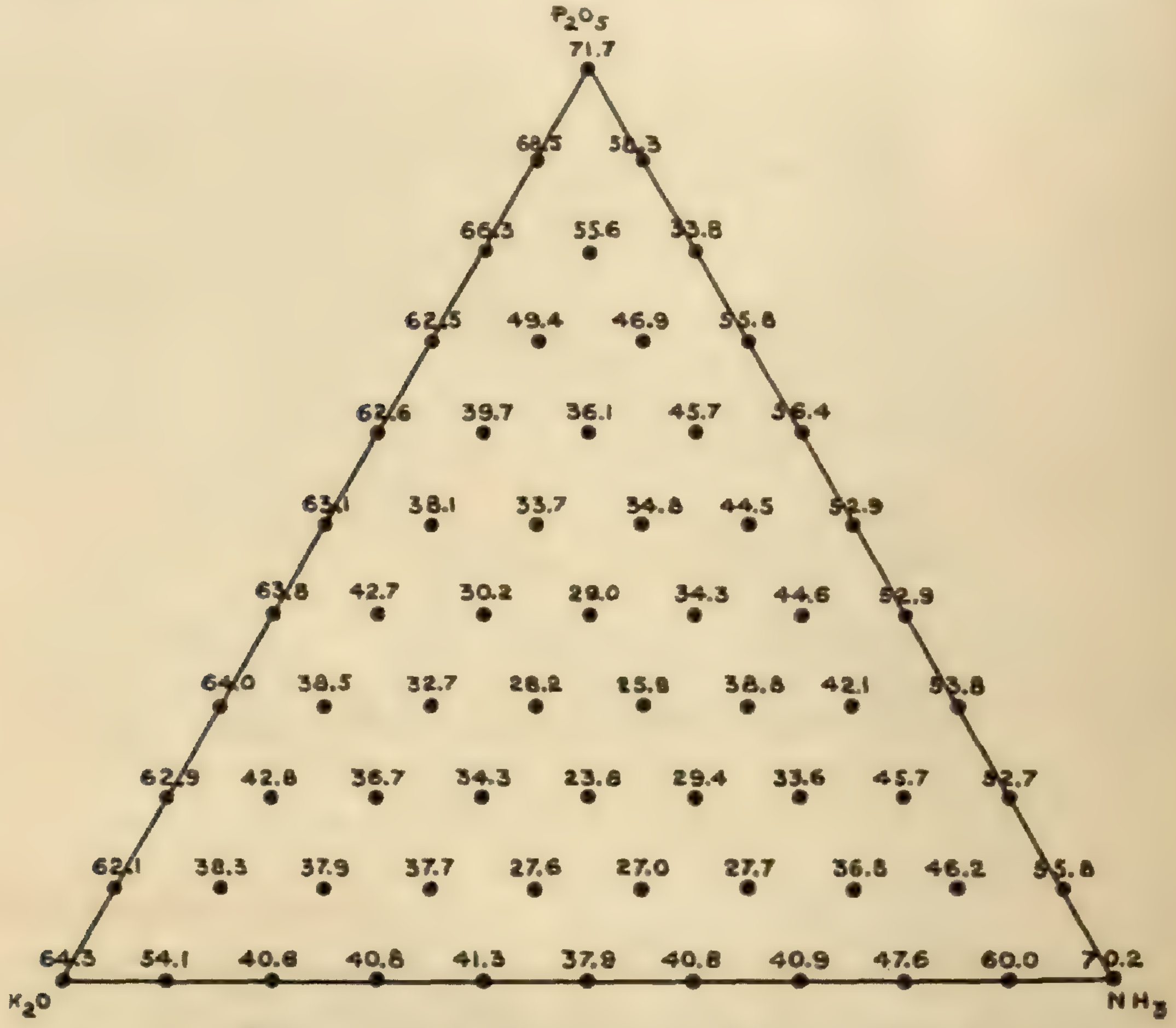

FIG. 4.—Showing the average concentration in parts per million of P_2O_5, NH_3, and K_2O of the solution after the growth of 10 wheat plants; concentration of the original solution was 80 ppm.

It may be shown mathematically that these three points lie upon a straight line and this is the case in the diagram.

The large dots in the diagram represent the original ratios corresponding to the scheme previously explained and given in fig. 1. The circles indicate the ratio left in the solution as shown by analysis. The other end of the line indicated by an arrow point shows the corresponding ratio of the removed materials. It must be borne in mind that

this diagram deals only with the ratios of the ingredients and not with the amounts that are present.

It is apparent that there is a decided tendency for these lines to converge toward a region somewhat below the center, as shown by the congregation of arrow points in this region. In other words, the solutions near this central area change least in their ratio, and the

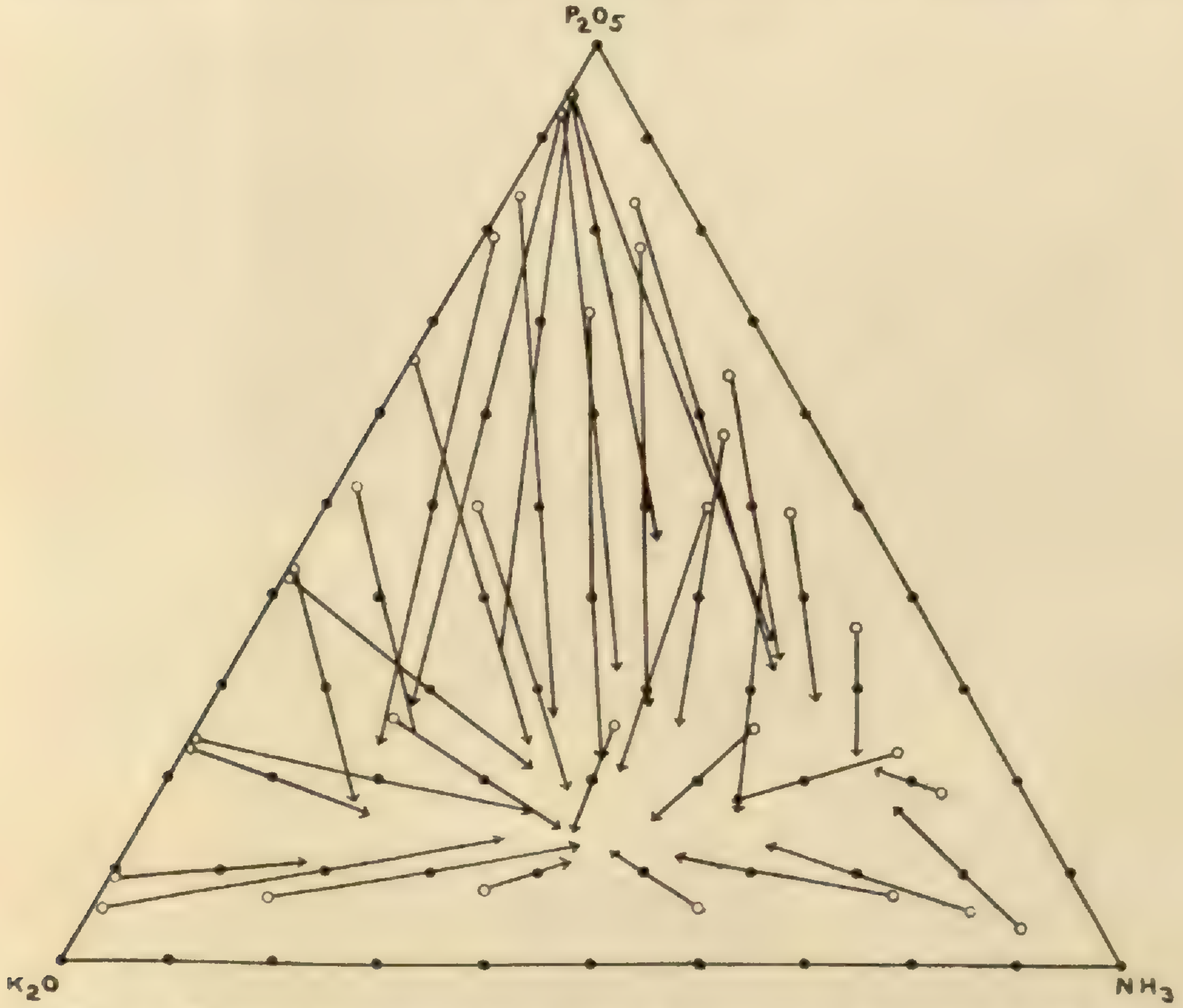

FIG. 5.—Showing the ratio of the original, the final, and the ratio of the loss of P_2O_5, NH_3, and K_2O from the culture solution: the dots indicate the ratio of the constituents in the original solution; the circles show the ratio of the constituents in the solution after growth; and the arrows show the ratio of the decrease.

farther the ratios were removed from this central area originally, the more were they altered in the course of the experiment. According to the diagram this area would seem to lie between the 10 and 20 per cent phosphate line, since the points on the lower line have moved in a direction opposite to that taken by the ratios in the upper part of the triangle. The data already presented show in general that the area of greatest growth occurred in this same region. It is in

this region of greatest growth, therefore, that the greater absorption took place with the least change in ratio; in other words, the solutions represented by this region offered the best environment for plant development and the best ratios for the absorption of plant nutrients.

Attention might also be called to the fact that in the ratios where the nitrate was low, there has been a movement to the no nitrate line, or at least so close to this line that it was impossible to plot them otherwise. After the comparatively small amount of nitrate was removed or reduced to a minimum, the point marking the ratio would have to move along the no nitrate base line in the direction either of the potash or of the phosphate, depending upon which was removed in the larger amount. The diagram shows that this movement of the ratio in the solutions was in nearly all cases toward the phosphate apex of the triangle. It is obvious that such a condition of affairs will cause a shifting of the lines connecting the ratios in the diagram, and that a similar state of affairs in the cultures on the low potassium line would produce a shifting of the ratio lines in the opposite direction. An examination of the diagram shows this has occurred, because the ratio lines in the upper part of the triangle show a divergence, giving a fanlike effect. In the case of the potash this divergence is also strongly noticeable, although the potash was never so completely removed as was the case with the nitrate.

The results of the experiments considered by periods

The very earliest periods, when compared with the later periods, show some differences in the ratio in which the three elements are removed, as has already been pointed out. Mention has been made of the fact that the ratios removed from the solutions along the lower phosphate line, namely, the 8 parts per million line of cultures, had a tendency to cause the ratio lines to turn from a point below this line to points above the line with increase in time. This general behavior of the cultures is very well shown by the three diagrams for the first, second, and third periods. The first diagram (fig. 6) shows the arrow points of the 10 per cent phosphate mixtures to lie below this line. The second diagram (fig. 7) shows some of the points above and some still below the line. In the third diagram (fig. 8) all but one arrow point lie above the line, and some arrow points of the 20 per cent

phosphate line are also noticed to have turned so far that some of them take a position even slightly above this line. There is a general tendency, moreover, for all of the points to lie somewhat higher for the other cultures, thus showing that this influence is probably common to all the cultures, though seen most strikingly in those containing small amounts, where an actual reversal takes place. This

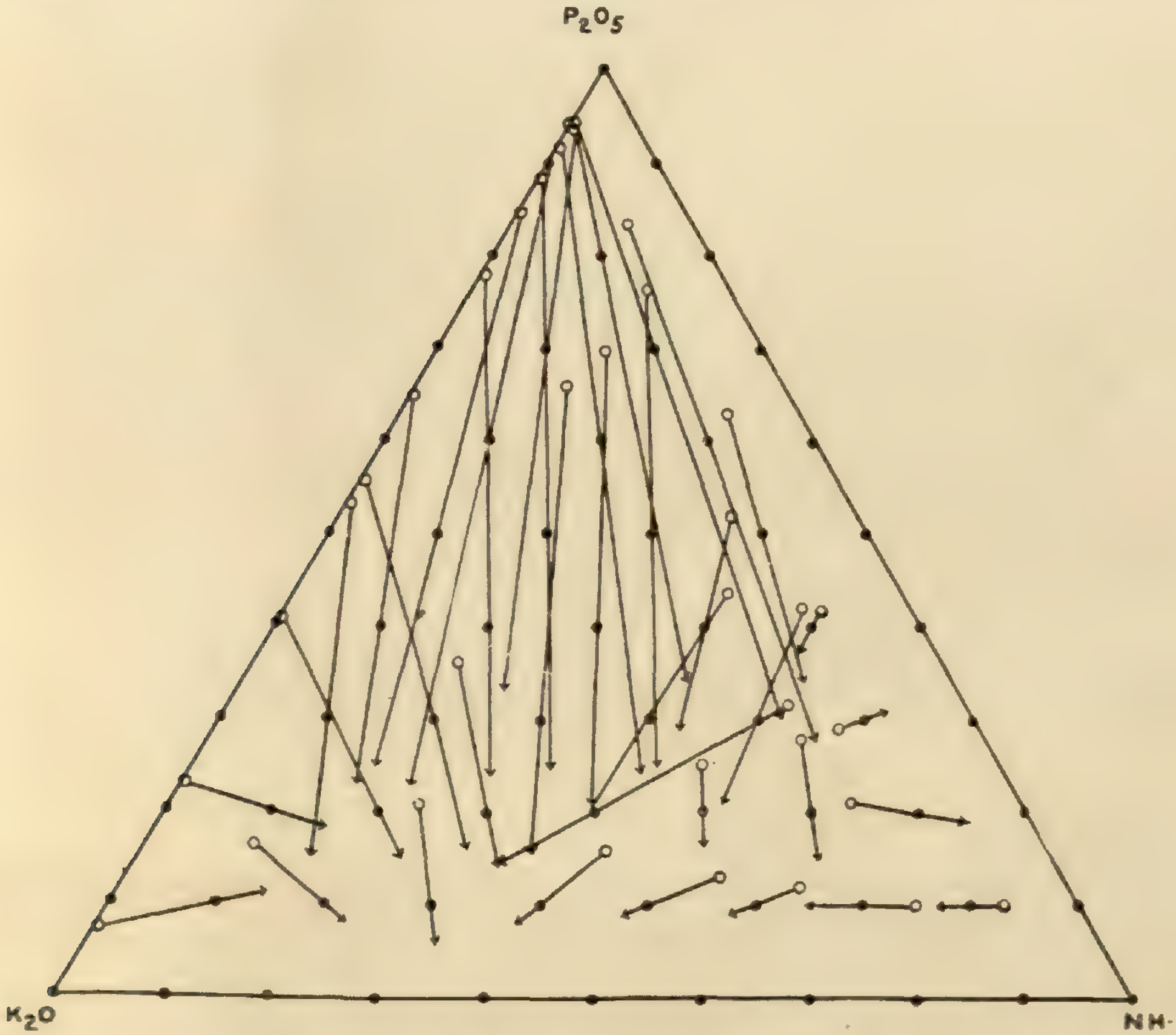

FIG. 6.—Showing the ratio of the original, the final, and the ratio of the loss of P_2O_5, NH_3, and K_2O from the culture solution in the first period.

general result may be interpreted to mean that the relative amount of phosphate removed in the early stages of the seedlings is not so great as it is subsequently, and the phenomenon can probably be correlated with the fact that in experiments where distilled water is used rather than these solution cultures, phosphate is excreted by the germinating seed and can be detected in the water in which germinating seeds or young seedlings bathe. Although the seedlings when used in these experiments have passed in the main through this

stage, the results show that there was a material lessening of the power to remove phosphate, probably due to the fact that the process of the phosphate absorption had not fully replaced the opposite function existing during germination and early growth.

The potassium absorption is also different from that in the later periods, although this is not so striking in the diagrams as in the case

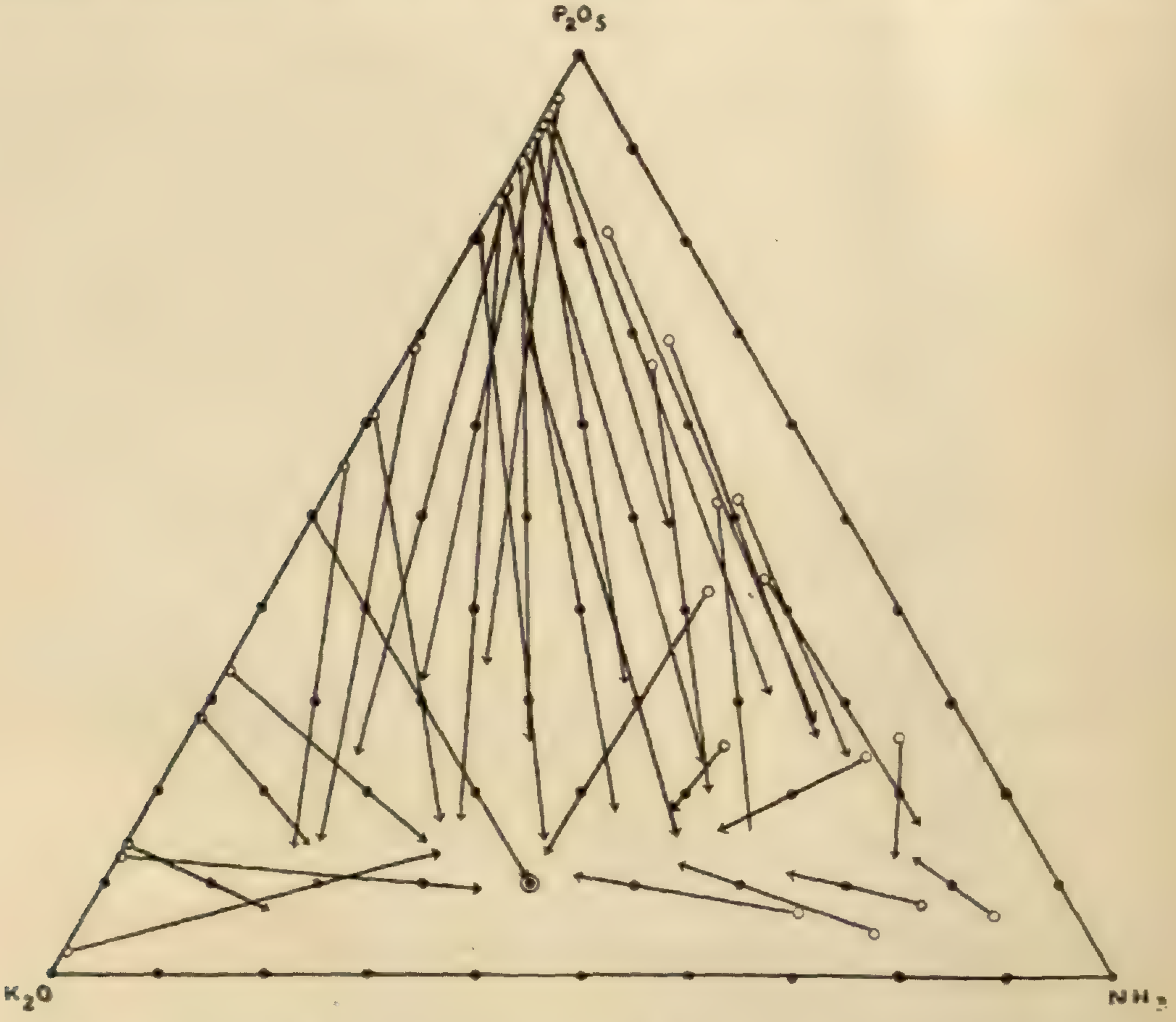

FIG. 7.—Showing the ratio of the original, the final, and the ratio of the loss of P_2O_5, NH_3, and K_2O from the culture solution of the second period.

of the phosphate. The average ratio of the removed material during these first three periods for all the cultures is 19 for phosphate, 39 for nitrate, and 42 for potassium; whereas the average for the five succeeding periods is 21 for phosphate, 44 for nitrate, and 35 for potash, thus showing that there is a tendency for a relatively greater potash and a relatively less phosphate absorption to take place during the earlier periods. So far as the influence of these fertilizer elements on growth is concerned, however, it is to be noticed that the nitrate has the

greatest effect, as is shown by the fact that the difference between the no nitrogen line and the 8 ppm. line is very great in the case of the nitrate, less in the case of the potash, and least in the case of the phosphate. As a rule, beyond the second or perhaps the third period the diagrammatic representation of the result is on the whole uniform, but is influenced undoubtedly by the conditions of growth during any

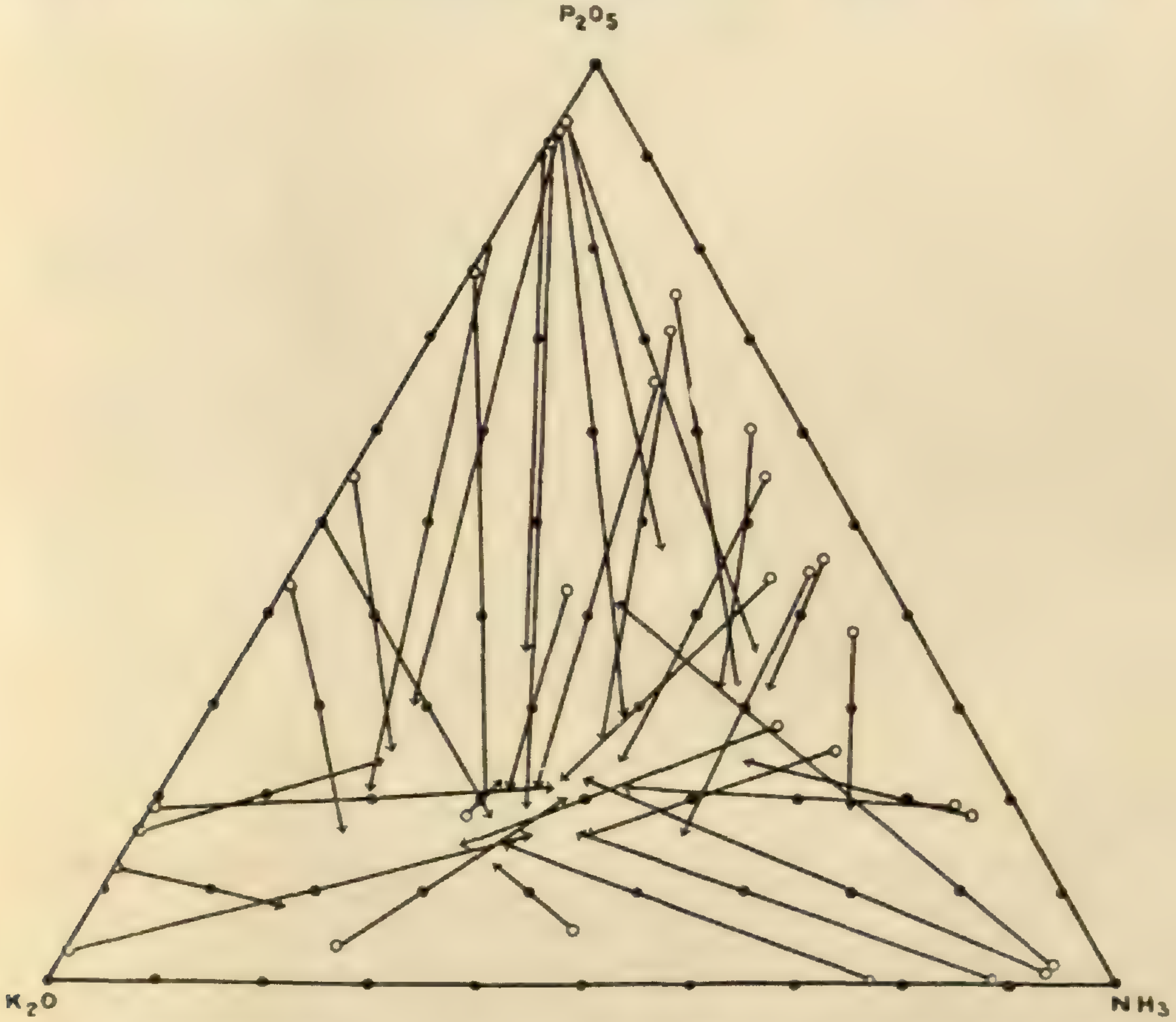

FIG. 8.—Showing the ratio of the original, the final, and the ratio of the loss of P_2O_5, NH_3, and K_2O from the culture solution in the third period.

period; in other words, by weather and other conditions, which is shown perhaps the quickest in the nitrate removal from the cultures.

Some remarks should here be made concerning the possible influence of bacteria. In the course of these experiments bacteria and other microorganisms were excluded so far as possible, but no special effort was made to maintain absolutely sterile conditions, inasmuch as this would have been a practical impossibility in an experiment on so large a scale. Moreover, it may even appear questionable whether

absolute sterility would be desirable. The bottles were sterilized before being used in making culture solutions for the various changes, the pans and other apparatus used in germinating the seed were sterilized from time to time, and corks used for the cultures were always clean and sterilized before use. Although all of these precautions were taken, it was of course not possible to exclude some microorganisms in such work, as the solutions were exposed from time to time to the air. There was in no case any excessive microorganic life noticeable. While bacteria and other microorganisms were present in the cultures to a slight and, under the conditions, unavoidable extent, it can hardly be said that their influence could have been large; that is, such influence as they had was probably so slight as to be negligible so far as the general and larger tendencies which are shown in this paper to exist are concerned.

Controls which were set up without having plants grown in them were found not to have changed their concentration or proportions of the constituents. Moreover, the various cultures support each other in their general tendencies. If the disappearance of nitrates were to be ascribed to bacterial activity, this should have shown itself all the more prominently as the age of the cultures increased. Such changes as were noticed from period to period might be ascribed to changes in the climatic conditions, thus still further affecting the plant's metabolism. This is very nicely illustrated in a series of preliminary experiments in which the solutions were changed every day instead of every three days, as was finally done. The diagram giving the results obtained on a clear day shows strikingly a relatively greater nitrogen removal under these conditions. The diagram giving the results obtained on the following day, which was cloudy and rainy, shows no less strikingly that relatively less nitrogen was absorbed on the cloudy and rainy day. It would be obviously unfair to conclude that under such conditions bacterial activities had been greater on the sunny day than on the following rainy day, especially as this result is in harmony with all observations on the removal of nitrate from solutions by plants. The processes of nitrogen utilization within the plant are known to be greater under conditions of better illumination. It is fair to assume, therefore, that this same general tendency held in all the other cultures, and that whatever

effect the bacteria may have had, it was slight in comparison to the activities of the plant itself under the conditions of this experiment.

Relation between growth and concentration of P_2O_5, NH_3, and K_2O found in the various cultures

The experimental results reported seem worthy of a closer analysis than that accorded them thus far. General tendencies as indicated

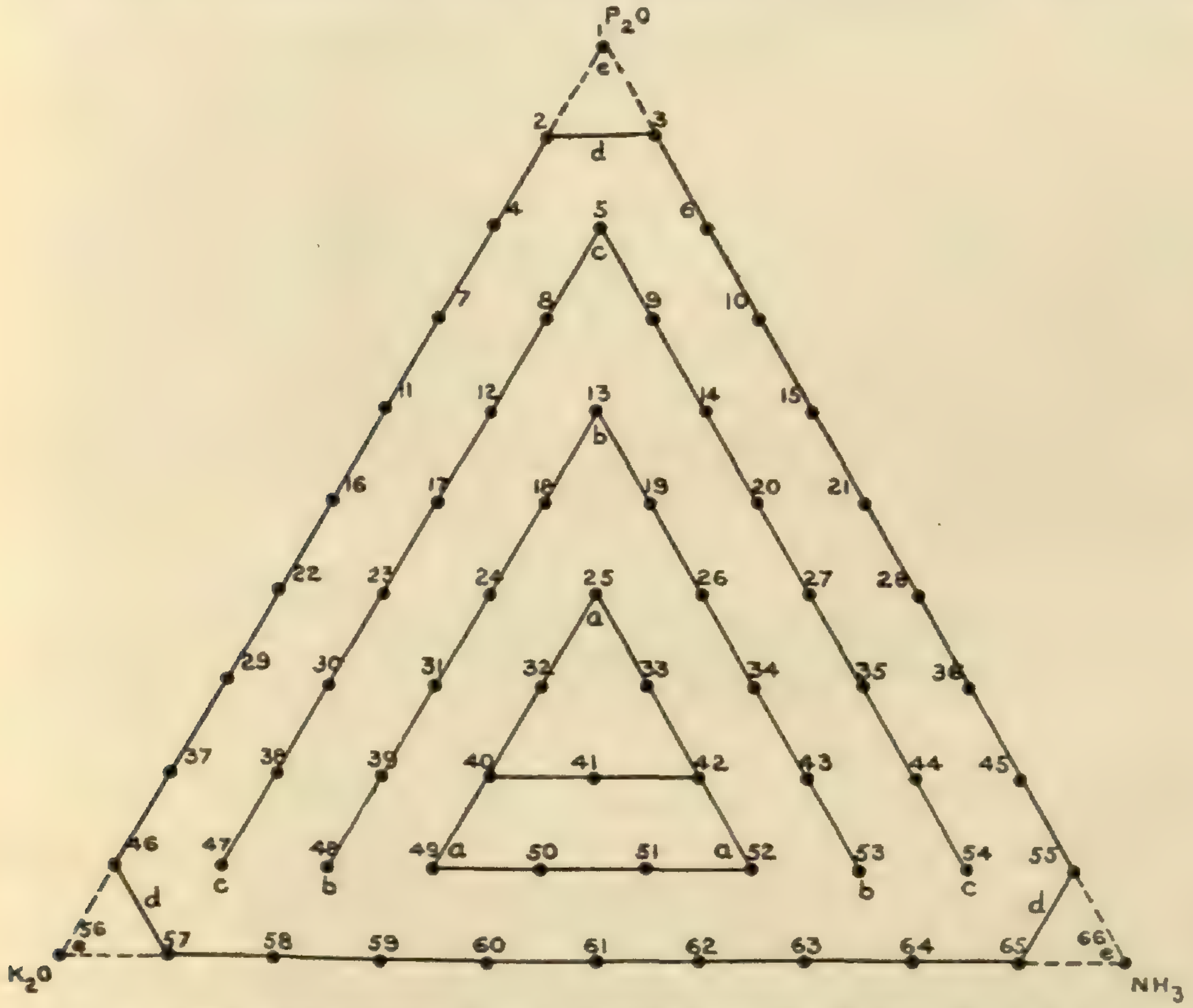

FIG. 9.—The arrangement of the culture solutions in groups: *a*, *b*, *c*, three fertilizer element groups; *d*, two fertilizer element group; *e*, one fertilizer element group.

by the individual cultures have already been pointed out, and these general impressions gleaned from the individual results can be better shown by a method of grouping. This method of grouping should be particularly valuable in showing the general tendencies, either in regard to plant growth or concentration differences connected therewith. Such a system of grouping, comparing different regions of the diagram, can be made in various ways.

The grouping shown in fig. 9 was made because by so doing the area of the greatest growth, which was always somewhat below the center of the triangle, will fall in these experiments into the central group. This central grouping is shown in the diagram as group *a*, the connecting lines showing the cultures included in this group. Group *b* takes in the cultures lying immediately outside of this central group. The same applies to group *c*, which is, however, farther removed from the central group. It will be noticed that these three groups contain the three fertilizer constituents. The next or fourth group contains all of the cultures in which two fertilizer elements occur, as shown by the lines. The fifth and last group consists of the sum of the single fertilizer elements. In handling the data, therefore, the average green weight in grams for each of these groups was determined, together with the average final concentration in the respective fertilizer constituents, or their combinations. In table I the average green weight and combined concentration of P_2O_5, NH_3, and K_2O is shown.

TABLE I

AVERAGE GREEN WEIGHT AND CONCENTRATION OF $P_2O_5+NH_3+K_2O$ OBTAINED IN DIFFERENT REGIONS OF THE TRIANGULAR DIAGRAM FIG. 9

(ppm. = parts per million)

CULTURE SOLUTIONS	NUMBER OF CULTURES INCLUDED	AVERAGE GREEN WEIGHT IN GRAMS	RELATIVE GREEN WEIGHT	AVERAGE P_2O_5, NH_3, AND K_2O		
				Original ppm.	Final ppm.	Percentage removed
Three fertilizer elements, group *a*	10	4.645	100	80	29.0	63.8
Three fertilizer elements, group *b*	11	4.120	88	80	35.0	56.3
Three fertilizer elements, group *c*	15	3.507	75	80	44.1	44.9
Two fertilizer elements	27	2.155	46	80	54.1	36.1
One fertilizer element	3	1.502	34	80	68.8	14.0
Three fertilizer elements, groups combined	36	4.010	..	80	37.0	53.8
All cultures combined	66	3.137	..	80	45.4	43.2

In the third column the relative green weight for the different groups is given, taking the results in group *a* as 100. From this it will be seen that the growth in group *b* is 88 per cent of that in group *a*, group *c* is 75 per cent; in the two fertilizer element group it is 46 per cent, and with the single fertilizer element the average result is only

34 per cent. The concentrations in these various groups are shown in the fifth column; the original concentration in all these cases was 80 parts per million of the combined constituents. In the first group, which was the one giving the greatest growth, the concentration was decreased from 80 to 29 parts per million, although, as has already been shown, the ratio of the three constituents in the solutions of this group suffered less change than did the ratio in the other groups. This can be seen from the diagram in fig. 5. In the second group the concentration was reduced to 35 parts per million; in the third group of the three fertilizer constituents to 44 parts; in the group of two fertilizer constituents it was reduced to 54 parts per million; and in the group containing one fertilizer constituent it was reduced to only 69 parts per million as an average.

For the sake of comparison, a group containing all cultures having the three fertilizer elements, as well as the combination of the entire group of sixty-six cultures, is given. The table also very clearly shows the markedly different effects produced on the green weight by a single fertilizer element and when these are used in combinations of two and of three, the results being approximately 1.5, 2.2, and 4.0, respectively, the higher group within the latter being as high as 4.6.

It will also be of interest to consider this same grouping in respect to the concentrations of the fertilizer elements individually. The number of cultures included in the group where two fertilizer elements were used was necessarily reduced, inasmuch as the ingredient in question did not occur in nine of the solutions, and the group of single fertilizer elements becomes, of course, reduced to only one culture, and for this reason has very little comparative value, although the result is usually decided enough to allow no doubt as to the general effect.

In the fifth column of table II is given the concentration of P_2O_5 found after growth, the original concentration being given in the fourth column for comparison. In the last column is shown the percentage decrease in the concentration of P_2O_5. This percentage decrease was in the first group 50 per cent, in the second group 37 per cent, and in the third group 27 per cent. In the combination of two fertilizer elements, one of which was phosphate, it

was 17.5 per cent, and in the phosphate by itself it was only 10 per cent. The actual decrease in concentration appears from the figures, however, to be strikingly uniform, varying in the different groups from 7 to 9 parts per million. This relationship of final to original concentration, however, is not properly shown by this form of grouping

TABLE II

AVERAGE GREEN WEIGHT AND CONCENTRATION OF P_2O_5 OBTAINED IN DIFFERENT REGIONS OF THE TRIANGULAR DIAGRAM FIG. 9

CULTURE SOLUTIONS	NUMBER OF CULTURES INCLUDED	AVERAGE GREEN WEIGHT IN GRAMS	RELATIVE GREEN WEIGHT	AVERAGE P_2O_5		
				Original ppm.	Final ppm.	Percentage removed
Three fertilizer elements, group *a*	10	4.645	100	16.0	8.0	49.7
Three fertilizer elements, group *b*	11	4.120	88	26.0	16.3	37.3
Three fertilizer elements, group *c*	15	3.507	75	34.0	24.9	26.9
Two fertilizer elements	18	1.531	33	40.0	33.0	17.5
One fertilizer element	1	0.648	14	80.0	71.8	10.3
Three fertilizer elements, groups combined	36	4.010	..	26.6	17.6	33.8

and can be much more satisfactorily handled, as will be done later, by grouping only such phosphate solutions as have the same original concentration. In the present table the original concentration is really an average of points varying, for instance, in the third group from 8 to 64 parts per million in phosphate content, giving the average concentration of 34 parts per million shown in the table.

TABLE III

AVERAGE GREEN WEIGHT AND CONCENTRATION OF NH_3 OBTAINED IN DIFFERENT REGIONS OF THE TRIANGULAR DIAGRAM FIG. 9

CULTURE SOLUTIONS	NUMBER OF CULTURE SOLUTIONS	AVERAGE GREEN WEIGHT IN GRAMS	RELATIVE GREEN WEIGHT	AVERAGE NH_3		
				Original ppm.	Final ppm.	Percentage removed
Three fertilizer elements. group *a*	10	4.645	100	32.0	9.8	69.4
Three fertilizer elements, group *b*	11	4.120	88	26.9	7.9	70.4
Three fertilizer elements, group *c*	15	3.507	75	22.5	5.8	59.9
Two fertilizer elements	18	2.721	58	40.0	22.8	43.1
One fertilizer element	1	2.752	34	80.0	70.2	12.2
Three fertilizer elements, groups combined	36	4.010	..	26.6	8.9	66.5

In table III is given the same character of results as have been given in the preceding section for phosphate, except that the concentration of nitrates is considered.

In the groups of two and single fertilizer elements, only those cultures containing nitrate are considered. In the three groups comprising the three fertilizer ingredients, the percentage decrease in nitrate is seen to be respectively 69, 70, and 60; in the two fertilizer element group it is 43; and in the single element, 12.

In table IV are given the results for the potash concentrations, similarly arranged and grouped as in the preceding tables.

TABLE IV

AVERAGE GREEN WEIGHT AND CONCENTRATION OF K_2O OBTAINED IN DIFFERENT REGIONS OF THE TRIANGULAR DIAGRAM FIG. 9

CULTURE SOLUTIONS	NUMBER OF CULTURES INCLUDED	AVERAGE GREEN WEIGHT IN GRAMS	RELATIVE GREEN WEIGHT	AVERAGE K_2O		
				Original ppm.	Final ppm.	Percentage removed
Three fertilizer elements, group *a*	10	4.645	100	32.0	10.8	66.2
Three fertilizer elements, group *b*	11	4.120	88	26.9	11.3	58.0
Three fertilizer elements, group *c*	15	3.507	75	22.9	9.6	58.3
Two fertilizer elements	18	2.212	48	40.0	26.1	34.8
One fertilizer element	1	1.106	24	80.0	44.3	44.6
Three fertilizer elements, groups combined	36	4.010	..	26.6	10.4	60.9

The percentage decrease in the cultures is for the three fertilizer elements in the three groups 66, 58, and 58, respectively; for the two fertilizer elements, 35; and for the single fertilizer element, 45.

Influence of different amounts of P_2O_5, NH_3, and K_2O, varying, respectively, from 8 to 80 parts per million

In the consideration of the results up to this point, no special discussion has been made in regard to the actual amounts of the individual fertilizer ingredients which were in the cultures. By reference to the original description of the diagram fig. 1 it will be seen, for instance, that there was a series of cultures in the line from number 46 to number 55 which contained 10 per cent of phosphate in the fertilizer mixture, or 8 parts per million of the culture solutions. Similarly, the line 37 to 45 contained 16 ppm.; the line 29 to 36, 24 ppm.;

and so on to the apex of the triangle. In the same manner, the line of cultures from 3 to 57 contained 8 ppm. NH_3 as nitrate; the line 6 to 58, 16 ppm.; and so on up to 80 ppm. NH_3 in culture 66. The line of cultures from 2 to 65 contained 8 ppm. K_2O; line 4 to 64, 16 ppm.; and so on up to 80 ppm. K_2O in culture 56.

It will be interesting to see what effect these different amounts of each fertilizer ingredient have had on the growth of the plant, and the removal of this constituent during the period of growth. In such

TABLE V

SHOWING THE RESULTS OBTAINED FOR P_2O_5 IN THE CULTURES CONTAINING DIFFERENT AMOUNTS OF P_2O_5 (PPM. = PARTS PER MILLION)

PERCENTAGE OF P_2O_5 IN FERTILIZER MIXTURE	PARTS PER MILLION P_2O_5 IN SOLUTION	AVERAGE CONTENT OF P_2O_5 IN FINAL SOLUTION, PPM.	AVERAGE DECREASE OF P_2O_5		AVERAGE GREEN WEIGHT	P_2O_5 DECREASE PER UNIT OF GREEN WEIGHT
			ppm.	percentage		
100	80	71.8	8.2	10.3	0.648	12.7
90	72	61.5	10.5	14.6	1.226	8.6
80	64	54.1	9.9	15.5	1.983	5.0
70	56	46.2	9.8	17.5	2.580	3.7
60	48	37.8	10.2	21.3	3.045	3.3
50	40	29.2	10.8	27.0	3.340	3.2
40	32	22.2	9.8	30.6	3.295	3.0
30	24	16.2	7.8	32.6	3.308	2.3
20	16	9.2	6.8	42.5	3.558	2.9
10	8	2.9	5.1	63.8	3.640	1.4
0	0	....	....	....	3.135	...

consideration it must always be borne in mind that there were present at the same time varying quantities of the other fertilizer constituents. For the purpose of such a comparison, the growth and concentration in the cultures along any of these lines has been studied and is presented in this section. With this in view all the results obtained in the various cultures in any one line were added together, and as the number of cultures naturally differ from line to line, the average was determined in each case for comparison, although this average is not intended to mean that all the cultures along this line were similar, for it has already been shown that in general the points in the middle were higher than those at the end of any one of these lines.

PHOSPHATE.—In table V are given the results obtained for P_2O_5 in the cultures containing different amounts of P_2O_5, varying from 80 to 8 ppm., as shown in the second column of the table.

The first column gives the percentage composition of the fertilizer mixture so far as the P_2O_5 content was concerned. In the third column is given the average concentration for the eight three-day periods in the experiment, and in the fourth column, the difference between this and the original concentration, thus giving the average decrease, which is expressed as a percentage in the fifth column on the basis of the original concentration. The sixth column gives the average green weight obtained along any of these concentration lines, and the next column gives the decrease in P_2O_5 calculated to the unit basis of one gram production of green plant. In other words, the decrease recorded in the fourth column has been divided by the green weight corresponding thereto in the sixth column. This gives, as it were, the rate of decrease in parts per million of the solution for each gram of green weight produced; but if it is desired to have the result expressed in terms of milligrams of P_2O_5 removed by each gram of green weight produced, the figures in the column must be multiplied by 2, since 250 cc. of solution were presented to the plants eight times; i.e., a total of 2000 cc. It will be noticed that the green weight steadily increased as the phosphate content decreased. It must be borne in mind, of course, that when the phosphate content decreases, there is a corresponding increase in the average content of both potash and nitrogen. In the last figure for the green weight, however, namely that in which the phosphate content became zero in the culture solutions, there is again a marked drop, although the potash and nitrogen content in these was higher than in any of the solutions above this in the table. It follows accordingly that a very distinct part was played by the phosphate in producing growth, although its maximum efficiency seems to be reached in these experiments in rather low concentration. Attention might also be called here to the fact that the concentrations of phosphate in soil solutions are always low, and relatively much lower than any of the other constituents here considered. The plant in its natural environment, therefore, has adapted itself to the occurrence of this constituent in weak solutions.

The increase in green weight shown by the table to be from 3.1 to 3.6 grams corresponded to an increase from 0 to 8 ppm. in the original P_2O_5 content. The further increase to 16 ppm. P_2O_5 has

produced no further increase in plant growth, and above this a decrease has even followed, which may be in part due to some direct influence of the phosphate solution, the carrier here used being calcium acid phosphate, and may also be due in part to the fact that the quantities of potash and nitrate are being decreased as the phosphate increases. This relation, however, has been discussed in a much more thorough manner where the ratios of these substances are considered, and the change in concentration which the solutions undergo, as shown in the diagram of ratio change in fig. 5, makes this matter very clear. It is there shown that the region of better growth is found in the lower part of the diagram, and this is also the region of most absorption and least change in the ratio. All these regions it will be noticed comprise solutions which contain low amounts of P_2O_5.

The average concentration of phosphate in the culture solution after growth, as shown in the third column, continually decreases. The actual decrease in the next column, however, shows that the greatest decrease in concentration of this element does not go with the greatest growth, but is found in the 40 ppm. phosphate solutions, increasing steadily from the 8 ppm. solution to this point, and then becoming practically constant up to the point where the other fertilizer elements entirely disappear and only phosphate remains, when it again drops slightly, the conditions for growth also being much poorer through this total absence of potash and nitrogen. The decrease when expressed as a percentage of the amount of material originally present shows that the removal is the more complete as the original concentration is lower. The last column in this section of the table, giving the decrease per unit of green weight, shows that equal weights of green plants cause quite unequal decreases in concentration, this change being least in the weaker solutions and greatest in the higher, thus indicating that more was removed by the plant in the higher concentrations than it could economically utilize under the conditions; i.e., the plant absorbed the material because it was there, although it apparently had already all that it could utilize economically. This is a fact consistent with field observations and ash analysis, where it is frequently noticed that the actual amount of mineral constituents is larger in the poorer plants.

NITRATE.—Table VI gives the results obtained for nitrate in the cultures containing different amounts of nitrate, similarly arranged and computed as in the phosphate table just discussed.

TABLE VI

SHOWING THE RESULTS OBTAINED FOR NH_3 IN THE CULTURES CONTAINING DIFFERENT AMOUNTS OF NH_3 (PPM. = PARTS PER MILLION)

PERCENTAGE OF NH_3 IN FERTILIZER MIXTURE	PARTS PER MILLION OF NH_3 IN SOLUTION	AVERAGE CONTENT OF NH_3 IN FINAL SOLUTION, PPM.	AVERAGE DECREASE OF NH_3		AVERAGE GREEN WEIGHT	NH_3 DECREASE PER UNIT OF GREEN WEIGHT
			ppm.	percentage		
100	80	70.2	9.8	12.3	2.752	3.6
90	72	54.2	17.8	24.7	2.699	6.6
80	64	42.0	22.0	34.3	3.046	7.2
70	56	32.8	23.2	41.4	3.169	7.3
60	48	24.1	23.9	49.8	3.492	6.8
50	40	18.3	21.7	54.2	3.685	5.9
40	32	12.0	20.0	62.5	4.166	4.8
30	24	6.1	17.9	74.6	3.852	4.6
20	16	0.5	15.5	96.3	3.893	4.0
10	8	0.2	7.8	97.5	3.156	2.5
0	0	....	....	....	0.995	...

The green weight column differs from the one discussed in the phosphate table in that the highest result occurs with the 32 parts per million NH_3 line, the numbers descending in each direction from his higher green weight. The change from 0 to 8 ppm. NH_3 is very marked in the green weight, which increases from approximately 1.0 gram to 3.2 grams, an even greater change than was noted in the phosphate table. The average decrease in concentration was in this case greatest between the limits of 32 to 64 ppm., the increase being gradual from the 8 ppm. solution up to the 32 ppm. solution, then being practically uniform up to 64 ppm., when it again declines. The figures in the percentage decrease column are on the whole much greater than those in the corresponding column in the phosphate table, thus showing a comparatively greater decrease of the nitrogen than of the phosphate in solutions of equal content of these elements, respectively. The last column, showing the rate of decrease per unit of green weight, shows the same general tendency for these figures to decrease with the decline in the original content of nitrogen in the solutions, as was noticed in the phosphate table, except that

the first two results, namely in the 80 and 72 ppm. solutions, are in this case lower than the following three or four entries, while in the phosphate table these two were the highest in the column. The conditions for growth with the phosphate in these two solutions, or groups of solutions, were very poor as compared with the rest of the results, while with the nitrate this difference in growth was not so apparent.

POTASSIUM.—In table VII are given the results obtained for potassium, the table being arranged and the results computed in the same manner as with those in preceding tables.

TABLE VII

SHOWING THE RESULTS OBTAINED FOR K_2O IN THE CULTURES CONTAINING DIFFERENT AMOUNTS OF K_2O (PPM. = PARTS PER MILLION)

PERCENTAGE OF K_2O IN FERTILIZER MIXTURE	PARTS PER MILLION OF K_2O IN SOLUTION	AVERAGE CONTENT OF K_2O IN FINAL SOLUTION (PPM.)	AVERAGE DECREASE OF K_2O		AVERAGE GREEN WEIGHT	K_2O DECREASE PER UNIT OF GREEN WEIGHT
			ppm.	percentage		
100	80	64.4	15.6	19.5	1.106	14.1
90	72	54.1	17.9	24.8	1.922	9.3
80	64	40.6	23.4	36.5	2.661	8.8
70	56	36.9	19.1	34.1	2.890	6.6
60	48	28.9	19.1	39.8	3.222	5.9
50	40	20.6	19.4	48.5	3.600	5.4
40	32	11.5	20.5	64.0	3.929	5.2
30	24	6.2	17.8	74.2	3.877	4.6
20	16	3.9	12.1	75.6	3.538	3.4
10	8	3.1	4.9	61.3	3.172	1.6
0	0	....	....	....	1.978	...

The green weight column is in its general tendency very similar to that observed in the nitrate table, namely that the 32 ppm. cultures give the highest green weight. The figures representing the average decreases and percentage decreases, on the other hand, correspond in trend more closely with those shown in the phosphate table, this similarity being especially shown in the last column giving the rate of decrease per unit of green weight, in which a regularly descending column of figures is seen. In the case of the green weight, the change from the 8 ppm. solutions to those containing no potash whatever was, as in the other cases, very marked, and this drop in green weight was also distinctly noticeable in the solution where potash alone was present. The results given in the three columns in the tables showing

the rate of decrease per unit of green weight are consistent in showing that relatively more was absorbed when more was present, although the plant does not seem to have been able to utilize this increase economically in its growth. This tendency is especially marked in the case of phosphate and potash, although it is also shown to an appreciable extent in the case of nitrogen.

As will appear in future publications, this general method of experimentation was used for the purpose of studying the effect of individual soil contituents and other organic compounds by using them in uniform concentration in all the cultures of a triangle. In these studies it was necessary to grow a control set without the constituent to be studied, so that the foregoing experiment was in this manner repeated a number of times, and the general results thus obtained were in harmony with those here recorded.

Summary

In this study the growth relationships and concentration differences were observed between solution cultures in which the phosphate, nitrate, and potash varied from single constituents to mixtures of two and three in all possible ratios in 10 per cent stages.

The better growth occurred when all these nutrient elements were present, and was best in those mixtures which contained between 10 and 30 per cent phosphate, between 30 and 60 per cent nitrate, and between 30 and 60 per cent potash. The growth in the solutions containing all three constituents was much greater than in solutions containing two constituents, the solutions containing the single constitutent giving the least growth.

The concentration differences noticed in the solutions were also very striking, the greater reduction in concentration occurring where the greatest growth occurred.

The change in the ratios of the solutions and the ratios of the materials that were removed from the solutions showed that where the greatest growth occurred, as above outlined, the solutions suffered the least change in ratio, although the greatest change in concentration occurred.

The more the ratios in these solutions differed from the ratios in which the greatest growth occurred, the more were the solutions altered

in the course of the experiment, the tendency in all cases seeming to be for the plant to remove from any and all of these solutions the material in the ratio which normally existed where greatest growth occurred. This did not actually occur in all cases, owing to the unbalanced condition of some of the solutions.

The results show that the higher the amount of any one constituent present in the solution, the more does the culture growing in that solution take up of this constituent, although it does not seem able to use this additional amount economically.

In the very early periods the ratio of phosphate absorption is low and the potash absorption high, although in final growth the greater response is obtained with nitrate, indicating relatively low phosphate requirement and high potash requirement of the seedling plant.

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CONTRIBUTIONS TO THE LIFE HISTORY OF WIDDRINGTONIA CUPRESSOIDES

W. T. Saxton

(WITH PLATES I–III AND THREE FIGURES)

In a previous communication (**10**) the writer has pointed out certain peculiarities in this genus, and in the genus *Callitris*, which mark them off sharply from all other Cupressineae which have been investigated. Many phases of the life history have now been fully investigated in both genera, and in the main confirm the results previously published, although certain points require modification or correction. The investigation of both genera has been carried on simultaneously, the original intention having been to present the results in one paper; it has however been found that the differences between the two are more radical than was anticipated, and the present communication relates solely to *Widdringtonia*. A similar account of *Callitris* will be published very shortly (**11**), in which the results of both investigations will be discussed. The methods used have not differed materially from those previously employed.

1. The male cone

The sporophylls are arranged, like the leaves, in decussate pairs. Each sporophyll is peltate and bears four microsporangia[1] on the proximal side of its stalk. The output of spores from a sporangium is about 500. The structure of the sporophyll in a transverse section through the insertion of the sporangia is shown in fig. 1. The structure of the cone in radial longitudinal sections has already been figured (**10,** fig. 2). The anatomy of the sporophyll agrees exactly with that of *Callitris* and will be later described in that genus.

2. The female cone and the ovule

The young female cone consists of two spreading decussate pairs of sporophylls, each scale bearing seven or eight ovules on the proximal half of the upper surface, and close to the median ridge.[2] Each

[1] Masters (**6**) says 2–3.

[2] In *W. Schwarzii* only three ovules are borne on each scale.

megasporophyll is traversed by a large number of vascular strands and resin canals; near the top of the sporophyll the latter are evenly disposed all round the periphery, and inside each canal is a vascular bundle with the phloem on the side nearest the canal. On the lower (outer) surface of each scale is a small umbo.

The structure of the ovule before and shortly after pollination has already been described and figured[3] (**10,** figs. 1 and 3). The ingrowth of the micropyle-closing cells is not followed by septation in them, as it is for example in *Pinus*. A transverse section of the micropyle is shown in fig. 2, in which it may be seen that the opening is often not entirely closed by the ingrowth of these cells. This figure shows a most remarkable resemblance to a similar section of the micropyle of *Bennettites*, figured by LIGNIER (**6,** fig. 31), as pointed out to me by Professor SEWARD.

Some time after pollination the sporogenous tissue becomes evident. Seen in median section it appears as about 18 or 19 large cells with dense cytoplasm and large lightly staining nuclei, sharply marked off from the surrounding cells, which have vacuolate cytoplasm and smaller deeply staining nuclei. The position and structure of these cells are indicated in figs. 3 and 4. Their number[4] is about 64, possibly exactly that number, in which case they are not improbably formed by repeated simultaneous divisions of a single archesporial cell. It is however quite as likely that the number is somewhat less than 64, and that they have not a common origin from a single archesporial cell. They are all exactly alike when first differentiated, and their subsequent behavior indicates that they are spore mother cells, only one of which, however, is functional. Sometimes a single layer of tapetal cells may be seen a little later.

At a somewhat later stage, one of the central mother cells becomes a very little larger than the remainder, the nucleus also enlarges very slightly, and the wall becomes a trifle thicker than that of its neighbors. This is the functional megaspore mother cell. At about the same time the non-functional cells elongate somewhat, and certain peculiar

[3] The wings of the ovule were accidentally described (p. 166) as being only one cell thick. This is never the case, even close to the margin.

[4] Calculated on the assumption that the actual number is to the number seen in median section as $\frac{4}{3}\pi r^3$ to πr^2.

structures make their appearance at or near their ends. These structures appear as homogeneous dark brown bodies of various shapes, and may be conveniently called the "brown bodies" (fig. 5). That they are not produced artificially is clearly indicated by the fact that they are found only in the sporogenous tissue, and at first only in a very definite position at the two poles of the cells. Later they may be somewhat displaced from this position.

The only structures previously recorded as occurring in megaspore mother cells, with which the "brown bodies" might conceivably be correlated, are the "kinoplasmic centers" found in *Ginkgo* (CAROTHERS 1) and other gymnosperms. It seems unlikely, however, that the "brown bodies" are of this nature, especially as their existence has not been proved in functional mother cells. They seem to be entirely unstained by Delafield's hematoxylin, and show a marked resemblance in this respect, as well as in color and consistency, to certain nucleoli, although nucleoli usually stain deeply with this reagent. At about this time some of the cells in or near the central axis of the nucellus begin to break down or to elongate, no doubt in preparation for the rapid growth of the pollen tube and embryo sac (fig. 6).

3. Megasporogenesis

About a week after the events described have taken place the functional megaspore mother cell is found in synapsis (figs. 7 and 9), the surrounding cells retaining more or less their former character. No preparation has been obtained which shows either of the reducing divisions. Figs. 10 and 11 show a state of things rather difficult to interpret. The arrangement of the cells marked 1, 2, 3 in fig. 10, and the character of the nucleus of "1" as seen in fig. 11, at once suggest that "1" is the megaspore preparing for its first division, and that "2" and "3" are two sterile cells cut off in the heterotypic and homotypic divisions respectively. A comparison with figs. 12 and 13, which unquestionably represent two normal megaspores before the first division, indicates however that either this interpretation is not the true one or that the ovule was not normal.

In the preliminary account (**10**) a stage was figured which seemed to indicate a very large number of megaspores. Although every preparation of the same age showed an almost identical structure, it has

proved to be merely that characteristic of an ovule which is destined to be abortive.

It is uncertain whether three or four potential megaspores are formed, but it is quite certain that only one becomes functional. As shown in fig. 12, the surrounding cells begin to disintegrate so quickly that the other cells derived from the functional mother cell cannot be recognized. There is some indication that it is not the lowest megaspore which develops, as is usually the case, but no definite statement can be made. The wall of the mature megaspore is so thin that it can be distinguished only with great difficulty.

In fig. 13 a cell immediately above the megaspore shows one of the "brown bodies" very distinctly, and a part of this cell is drawn on a larger scale in fig. 14. Fig. 13 indicates that polarity may be established in the embryo sac before the first division of the megaspore nucleus, and many other preparations show the same, but by no means all (compare figs. 12 and 15).

4. The female gametophyte[5]

After the first division of the megaspore nucleus, the walls of the embryo sac and disintegrating mother cells can scarcely be distinguished. Their thickness has been unavoidably exaggerated in fig. 15. In the preparation figured (the only one showing a binucleate sac), no polarity is evident, nor are the nuclei arranged quite parietally. After the next division, however, the four nuclei are imbedded in (or rather protrude inward from) a very thin parietal layer of cytoplasm, and there is some indication of polarity, two nuclei being situated near the upper end and two near the lower end of the sac, the two pairs being symmetrically placed with regard to one another (fig. 16). This is distinctly interesting in view of the recently revived opinion that the embryo sac of angiosperms is derived from that of gymnosperms by a series of reductions, although it is to be noticed that certain "primitive" angiosperms do not show the polarity so characteristic of the vast majority. The growth of the embryo sac (prothallus) proceeds rapidly now toward the apex of the nucellus,

[5] As pointed out by COULTER and CHAMBERLAIN (2), the history of a gametophyte should start from the mother cell rather than from the spore, but practically it is more convenient to consider sporogenesis separately.

the apical part becoming very narrow and closely resembling the tip of an advancing pollen tube. The breaking down of certain cells in the axis of the nucellus, facilitating the upward growth of the prothallus, has already been referred to. The divisions of the nuclei are doubtless simultaneous until at least 64 are present (exactly that number having been counted in serial sections), and possibly until wall formation begins. Fig. 17 shows in outline the general structure of the nucellus at the time when 64 nuclei line the embryo sac. Fig. 18 is part of a tangential section of the prothallus after free nuclear divisions have ceased. The nuclei each contain a single nucleolus which can invariably be seen to be hollow.

Cell formation takes places as in most other gymnosperms, and has already been described and figured (**10,** fig. 9). A large number of nuclear divisions have been seen in the "alveoli," certain features of which strongly recall the peculiar divisions described by LAWSON (4) as occurring at this time in *Cryptomeria.* All the earlier phases (figs. 19 and 20) are quickly passed through, but that shown in fig. 21 is very persistent, the marginal fibers having almost the appearance of a cell wall. The wall between the nuclei, however, is always developed, but in cases where its width does not nearly equal the diameter of the cell, it is just possible that wall and fibers may disappear again and thus give rise to a binucleate cell. It has not been demonstrated, however, that binucleate cells ever originate in this way, and the chief interest of fig. 23 is in providing a connecting link between the very peculiar divisions giving rise to the temporarily binucleate cells of *Cryptomeria* and the ordinary mitotic divisions in normal conifer prothalli.

Very soon after cell divisions are complete, the archegonium initials make their appearance. These become considerably larger than the surrounding cells and their nuclei are a little larger (fig. 22). The position of the archegonia is somewhat variable, but usually two distinct types seem to be formed: (1) a single group of about ten or more, directly abutting on the swollen end of the pollen tube;[6] (2) one, or usually more than one, group of few or several archegonia (rarely a single archegonium) which are found near, but not abutting on, the upper part of the pollen tube, and deep-seated in the prothal-

[6] In the few cases where two pollen tubes reach maturity, a group of this kind is organized in connection with each tube.

lus (fig. 23). It is certain that neck cells are formed in the former (1), although they are very evanescent and much more difficult to demonstrate than in the archegonia of *Pinus*, for example; but they have not been demonstrated in the deep-seated archegonia (2), although it is not unlikely that this is merely due to the difficulty of differentiating them from other cells of the prothallus. In a recently published account of *Juniperus* (OTTLEY 9), a case is described and figured in which a small deep-seated archegonium occurred outside the normal group. The figure leads one to suppose that no neck cell could be demonstrated, but no statement on this point is made in the text. After fertilization no neck cells can be found in either type of archegonium, which accounts for the suggestion made in my former paper (10) that neck cells are never formed in *Widdringtonia*. The neck, where present, consists of a single tier of four cells (fig. 23).

The central nucleus of the archegonium divides (in the first type of archegonium) simultaneously in the whole group (fig. 24), a conspicuous spindle being organized with long, slender, and considerably twisted chromosomes (fig. 24). The reduced number of chromosomes (six) may be counted fairly readily in this division. It is to be noticed in fig. 23 that although the central nucleus of every archegonium in the basal group is dividing, yet the nuclei of the other archegonia are still in the resting condition. The evidence that these do not divide is purely negative, but the possibility of the deep-seated archegonia being really archegonium initials only, must not be overlooked. The case shown in fig. 16 of my former paper (10) indicated that rarely a persistent ventral canal nucleus is formed, but out of scores of prothalli examined, containing thousands of archegonia, this is the only case in which such a state of things was clearly indicated. In no other preparation has the ventral canal nucleus been certainly identified, although the occurrence of the spindle which initiates its formation furnishes additional evidence that it must be formed. Doubtless it is normally very evanescent. From STRASBURGER'S (12) figures of the same nucleus in *Juniperus*, it would seem that it is by no means a conspicuous object in that genus, and although LAWSON (5) figures a large ventral canal nucleus in *Thuja*, it evidently disappears quickly, as it is not figured in the mature archegonium, and the same was found in OTTLEY'S recent paper on *Juniperus* (9).

The formation of binucleate and multinucleate prothallus cells has already been described. It is initiated at about this time, but nuclear divisions continue to occur during the earlier phases of embryo formation. Two such dividing nuclei are drawn in figs. 26 and 27.

The structure of the mature archegonium is much like that of other Cupressineae, with a large, centrally situated oosphere nucleus and a basal (or sometimes partly lateral) vacuole (fig. 28). The neck cells do not persist long, the archegonia of the basal group finally opening into the pollen tube.

The total number of archegonia of both kinds organized in a prothallus varies considerably. Sometimes there are only about 25–30, usually about 40–70, and occasionally as many as 100. The microphotograph (text fig. 1) is taken from a tangential section of a prothallus in which about 100 archegonia were present. About 50 of these appear, cut transversely, in this section. A prothallus containing about 50 in all was sketched in my preliminary paper (**10,** fig. 15).

FIG. 1.—Microphotograph of a tangential section of a prothallus in which about 100 archegonia were present.

5. The male gametophyte

The earliest stages of the germination of the microspore have been already described, but the description will be briefly repeated here. The mature pollen grain is uninucleate and there is no evidence that any prothallial cells are formed. Thus the "pollen grain" is here synonymous with the "microspore." The earliest stage of germination usually consists in the formation of a solid outgrowth from the exospore, which applies itself closely to the surface of the nucellus, sometimes with a tendency to grow down between the nucellus and integument. About three pollen grains usually begin to germinate

in each ovule, but generally only one and never more than two reach maturity. A little later the solid outgrowth of the exine becomes hollow, and the intine then grows through it, forming the tube, which at once penetrates a short way into the nucellus, the single nucleus passing into the tube. Occasionally a tube is formed at once on germination.

The time during which the pollen tube remains uninucleate seems to vary a good deal, a tube with a single nucleus having been found associated with a four-nucleate prothallus (fig. 29), while in two or three cases a tube containing three nuclei was found in an ovule before the first division of the megaspore nucleus; one such case is shown in figs. 30 and 31. No differentiation of cytoplasm can be seen here around the upper nucleus, doubtless the body cell nucleus, but the preparation is noteworthy as the only one in which a difference in size could clearly be seen between the two sterile nuclei, that nearest the apex of the tube (the "tube" nucleus) being considerably larger. Fig. 32 is a detailed drawing of the tube, the position of which is shown in fig. 17. Its size is approximately the same as that of figs. 30 and 31, but the structure is somewhat different. The two sterile nuclei are precisely alike in every respect, as they are in every preparation in which they occur, except in the one noted above and in one abnormal tube referred to later. The body cell is here sharply demarkated from the surrounding cytoplasm in which the other nuclei are imbedded.

It should be mentioned here that the occurrence of only two nuclei in the tube at a stage somewhat later than this, as previously reported (**10**), has not been confirmed in any other preparations. It is curious that, in fact, the binucleate stage has never been certainly identified, as it is not improbable that the case just mentioned is really a three-nucleate tube, and that defective preparation is responsible for the appearance of only two. It may be added that the preparation there figured is from material collected very soon after the work was begun, and before the best fixing agents and oven periods had been satisfactorily ascertained. On the other hand, it may be that the uninucleate condition had persisted later than usual in this case, and that only two nuclei are actually present. In any event, it is certain that the two sterile nuclei must be cut off in somewhat rapid succession.

After they are formed, the pollen tube renews its activity and rapidly grows until it reaches the megaspore membrane. It is only rarely that the apex of the membrane is penetrated; more commonly the tube grows down a little farther before entering the prothallus. The entry is however almost invariably effected before the commencement of wall formation, the latter usually taking place only after the tube has taken up its final position. At the point where the pollen tube pierces the megaspore membrane, a slight constriction almost invariably occurs, while the tip of the tube dilates a little to form a kind of vesicle just within the prothallus. Preparations are often met with in which the contents of the tube are just opposite the constriction, indicating a certain amount of difficulty in passing this point. Inside the prothallus the wall of the tube becomes thicker (fig. 33). When the difficulty of passing this point is overcome, the tip of the tube rapidly advances to about, or a little beyond, the middle of the prothallus. During the whole later growth of the tube the individuality of the body cell is less evident than at the stage shown in fig. 32, and its cytoplasm may be quite indistinguishable from the rest of the tube cytoplasm. A case of this kind, in which all three nuclei are imbedded in a common mass of cytoplasm, has already been figured (**10,** fig. 10), and is not uncommonly met with (see also fig. 33).

Perhaps the most usual case is shown in figs. 34 and 35. Here the body cell is distinct, not only from the surrounding cytoplasm of the tube, but also from the cytoplasm in which the sterile nuclei are imbedded. With the triple stain, the cytoplasm of the body cell stains red, that in which the sterile nuclei are situated takes the orange, while the rest of the tube cytoplasm is a deep violet. In later stages the body cell increases very considerably in size. Its structure shortly before division has already been described and figured. Some uncertainty was expressed as to the fate of the two sterile nuclei. It was suggested that they were probably absorbed by and became indistinguishable from the cytoplasm. Later preparations have in the main supported this view, but sometimes these nuclei are recognizable in connection with a quite mature body cell, in a prothallus in which wall formation is complete.

Only a single preparation has been obtained showing the two male cells fully organized (figs. 36 and 37). Each cell is surrounded by

a definite wall (or membrane) and is more or less hemispherical. The cytoplasm is dense and very homogeneous, and in the center of each cell is a large nucleus with no nucleoli. The entire absence of starch in the male cells is noteworthy, as compared with other Cupressineae. In this preparation the two cells are just beginning to separate, and probably they would finally become rounded off as reported by LAWSON (4) in *Libocedrus*. In contact with one of these cells (see figs. 36 and 37) is a curious body which presents the appearance of a vesicle containing a number of small, deeply stained granules. No light can be thrown on the morphology or functions of this body. No trace whatever can be seen of the two sterile cells. Possibly their disappearance may be connected with the appearance of the vesicle, but this is merely conjecture.

6. Fertilization and embryogeny

The actual process of fertilization has not been seen in *Widdringtonia;* probably it agrees essentially with that in other Cupressineae as has been found to be the case in *Callitris.*

The first stage of the proembryo shows two free nuclei arranged lengthwise in the archegonium (fig. 38). The two nuclei are alike in size and structure. No starch is noticeable in the proembryo at this stage, but in all later stages seen, a considerable amount of starch is present. In later stages the structure has often been very difficult to interpret. Although a considerable number of preparations has been obtained, the sections have nearly always happened to be oblique. In two cases the following method has been successfully employed in order to get over this difficulty. Serial sections were drawn in ink on gelatin plates, the drawings being then placed together in sequence. If the thickness of the plates is to the thickness of the sections as the diameter of the drawing is to the diameter of the section, then a solid figure is obtained which represents accurately the object sectioned, the structure of which can be seen fairly clearly through the transparent gelatin. The gelatin plates can be easily stuck together by wetting them slightly.

Figs. 39 and 40 are reconstructed from serial sections. They show proembryos containing five and ten nuclei respectively. In fig. 39 delicate walls can already be seen between the nuclei, the

appearance of which indicates that they probably arose as cleavage planes. In fig. 41 a transverse section of the upper four nuclei is shown. The presence of kinoplasmic radiations (spindle fibers?) between these four nuclei indicates that probably they had a common origin and that after the first division of the oospore the basal nucleus remains undivided. It is evident that the early development of the proembryo does not show any resemblance whatever (after the first division) to that described by LAWSON (**5**) for other Cupressineae (*Thuja* and *Libocedrus*), and by OTTLEY (**9**) for *Juniperus*, where eight free nuclei are organized before walls are laid down.

Fig. 40 shows diagrammatically the structure of a ten-nucleate proembryo entirely filling the archegonium. It was not quite clear whether the walls extended to the upper three nuclei or not. The stages between figs. 39 and 40 are missing, and it is difficult to guess how the second form arose from the first. Probably there is some variation in the earlier divisions; compare, for instance, fig. 40 with the two proembryos figured in my preliminary account (**10,** fig. 16). Embryo development has already been briefly described.

Fig. 42 is a drawing of a germinating seed before the cotyledons are withdrawn from the testa. Fig. 43 shows the upper part of the same seedling after removal of the testa. Often the testa is carried up on the tip of one of the cotyledons in germination. The seedling structure (anatomy) of *Widdringtonia cupressoides* differs somewhat from that recently described by HILL and DE FRAINE for other species (**3**), and an account of it has already been published from this laboratory, together with a description of a remarkable twin seedling of the same species (MORRIS **8**).

In the plumular development a pair of opposite leaves succeeds the cotyledons, and is found in a plane perpendicular to that of the cotyledons. These leaves are followed by from about three to about ten alternating whorls of four leaves (text fig. 2). The structure and leaf arrangement of a tricotyledonous embryo have proved rather interesting. The three cotyledons are equal in size and have probably been equivalent in development and are succeeded by alternating whorls of three primordial leaves. This is shown in the photograph (text fig. 3). The transition region is longer than in the normal seedling, and only at its lower end is there any indication that the

three cotyledons are not all equivalent. Here two of the xylem groups grow somewhat smaller and approximate and finally join, thus giving the diarch root structure typical of the normal seedling.

7. Abnormalities

The tip of the pollen tube of fig. 23 contains a curious body cell which is shown more highly magnified in fig. 23*a*. Its appearance strongly suggests that it is not a normal body cell just after the division of the nucleus, but that during or immediately following the division disintegration of the nucleus has begun.

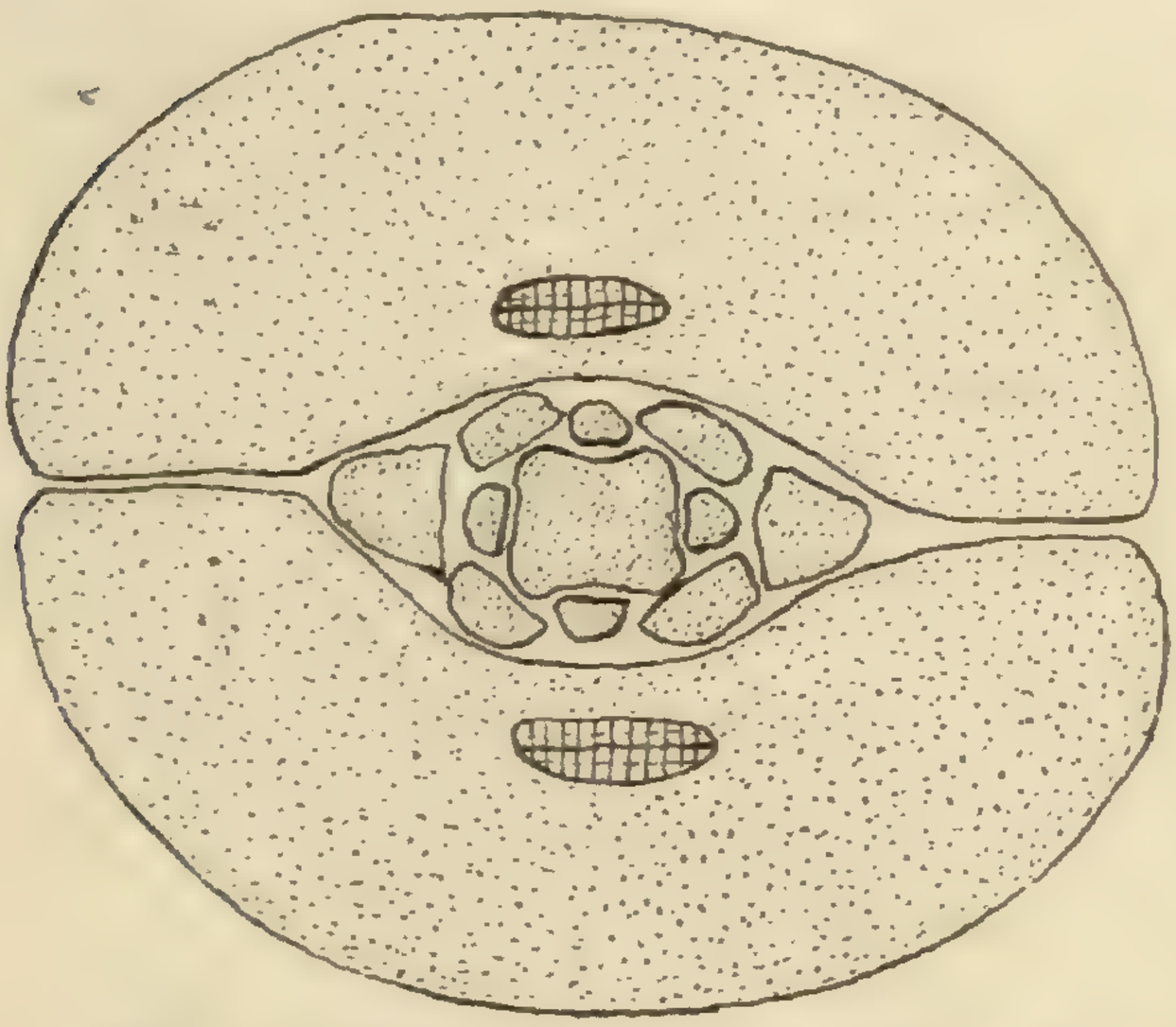

FIG. 2.—Diagrammatic cross-section of the cotyledons and plumule of *Widdringtonia*, showing arrangement of the primordial leaves in a dicotyledonous seedling.

In fig. 34 a slight irregularity is evident, inasmuch as a small fragment of the body cell nucleus has been constricted off and left just behind in the cytoplasm of the cell. It is barely possible that this may have been caused by defective preparation, but one other case has been seen in which a small papilla protruded in precisely the same direction from the body cell nucleus (not figured). Moreover, no such phenomenon has ever been seen by the writer in the case of any other large nuclei, either in *Widdringtonia* or any other plant.

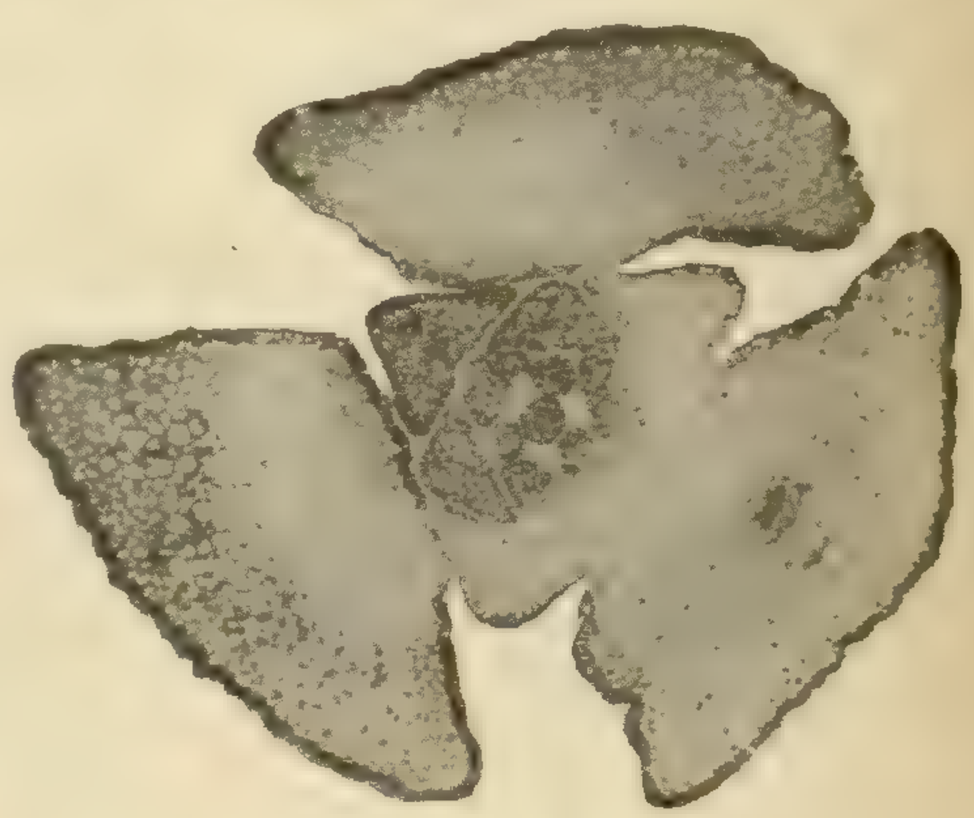

FIG. 3.—Photograph of a transverse section of a tricotyledonous seedling.

One very curious abnormal male gametophyte is shown in fig. 44. Here the sterile nuclei are in the swollen tip of the tube (which is surrounded by the usual group of archegonia), but the body cell has been left far behind. The nuclei are shown in more detail in figs. 44*a* and 44*b*. It is noticeable that the body cell does not exhibit such

a distinctive structure as is normally the case, while one of the sterile nuclei is clearly larger than the other and is also distinguished structurally from it. This also is unusual and suggests the possibility that this larger cell might have eventually taken the place of the tardy body cell.

The other two cases figured which seem to be abnormal are both taken from archegonia occurring in prothalli in which the pollen tube had lost its contents, but in which no proembryo was evident. Both might conceivably be taken to represent stages in the fusion of sexual nuclei. Fig. 45 shows an archegonium which was unhesitatingly considered to contain the sexual nuclei in contact, but on examination of these nuclei with a more powerful objective they were found to have the structure indicated in fig. 45*a*. The whole of the contents seems to consist of homogeneous and rather dense nuclear plasm except for the four nucleoli (?). Each of these nucleoli (?) consists of a membrane from the inside of which a plasmic strand has contracted on which are regularly arranged about six (three or four in optical section) very deeply staining bodies, of the shape and size figured. It is suggestive that the number of these bodies in each nucleolus (?) should be the same as the haploid number of chromosomes. It is also suggestive that two of these nucleoli (?), differing only in size, should be present in each of the fusing nuclei, if such they are.

Figs. 46*a* and 46*b* are two successive sections of the same archegonium nucleus. The structure is so strikingly different in the two that it is difficult to believe they are actually parts of the same nucleus; but the fact is clear. In each section all the deeply staining structures (chromatin granules? and nucleoli?) have been figured, whether or not they occur in the same optical focus.

Beyond the suggestion made above, I have no opinion to offer on these figures. Since they occur at such an interesting stage of the life history it seems desirable to place them on record.

8. General

Since much variation has been noticed among the Cupressineae in the time elapsing between pollination and fertilization, it is interesting to compare *Widdringtonia* in this respect. The chief point of interest is that although a very long period intervenes between

pollination and fertilization, yet there is no break in the continuity of development, such as probably occurs in those temperate conifers which are pollinated in one season and fertilized in the next. It is further interesting to notice that there are absolutely no fixed periods, so far as the writer can judge, when definite stages may be found. It may be not out of place to observe that these facts have made the working out of the life history very much more difficult than would otherwise have been the case, which must be the excuse for the gaps which still remain in the present account.

At the time of writing (November 1909), complete data are not available, but cones known to have been pollinated in January (or possibly early in February) of the present year are still far from ready for fertilization. They are still under observation and may probably be fertilized by the time this paper finally goes to press, in which case a postscript will be added.

Very young female cones may be found at any time, but soon die off unless pollinated. The time of appearance of the male cones is very variable. During the present year the writer has failed to find a single male cone, except in the early part of January. Nevertheless, recently pollinated ovules were collected at the end of June, so that there probably must have been male cones in the vicinity during May.

During 1908, male cones were collected in April and again in May (mature in both cases and separated by a full four weeks). A large number of trees were examined frequently and carefully during those months in 1909, without a single male cone being found. The following field notes of the different aged cones met with at one time and in one clump of trees may be of interest. About March 1 the following female cones were found: (1) very young; scales still widely open; pollinated (probably about one month previously); (2) medium size; still quite green; ovules with well-developed embryo sac; (3) full grown, brown, but with junction lines of scales still green; ovules with full-size embryo sac but no trace of cell formation; (4) full grown, uniformly light brown; integument discolored; young embryos; (5) dark brown, showing signs of dehiscence; mature seeds. It was afterward found that (3) could be segregated into two separate batches, in one of which fertilization took place about the end of April, in the other about the middle of September.

As stated in the introduction, it is not proposed to discuss the facts here reported until the corresponding facts in the life history of *Callitris* are published, when the two genera may conveniently be compared and contrasted.

Summary

The microsporophylls are arranged in decussate pairs and each bears four microsporangia.

The mature pollen grain is uninucleate.

The four equal megasporophylls are opposite and decussate.

About 64 megaspore mother cells are organized at the base of the nucellus, but only one is functional. Peculiar structures are noted at the poles of the non-functional megaspore mother cell.

The megaspore may show polarity before the first division of the nucleus, or when four nuclei are present. The divisions of the embryo sac nuclei are probably simultaneous.

Cell formation in the prothallus is normal in most respects, but certain peculiarities have been noted in the nuclear divisions which suggest comparison with *Cryptomeria*.

The archegonia are never situated at the apex of the prothallus, but in several groups organized in relation to the pollen tube and deep-seated in the prothallus. The lowest group abuts on the pollen tube; the upper groups do not, and may possibly represent archegonium initials. In the lowest group four neck cells are formed and a ventral canal nucleus is cut off. The total number of archegonia in a prothallus varies from about 30 to about 100.

The microspore nucleus remains undivided for a long time. In other respects the development of the male gametophyte is more or less normal, but the so-called "stalk" and "tube" nuclei are almost invariably exactly alike and tend to disappear completely in the mature pollen tube.

The proembryo completely fills the archegonium, but the arrangement of the cells is somewhat variable. Walls are formed when less than eight free nuclei are present.

The mature embryo has two (very rarely three) cotyledons.

The cells of the mature prothallus are all binucleate or multinucleate.

Stages in the life history are found not to correspond to definite seasons, and a long time elapses between pollination and fertilization.

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POSTSCRIPT (March 26, 1910).—Wall formation in the prothallus of ovules pollinated about January, 1909, is now taking place. Fertilization is likely to follow in the course of a few days. It may therefore be stated that an interval of fourteen or fifteen months will elapse, in this instance, between pollination and fertilization.

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[7] A considerable number of papers bearing on the subject were quoted in my former paper. It is not necessary to repeat the titles here, only those actually cited in the text being given.

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EXPLANATION OF PLATES I–III

All figures were drawn with Zeiss camera lucida, microscope, and lenses, except figs. 39 and 40 (see text). In all: *b*, "brown bodies"; *c*, micropyle closing cells; *d*, megaspore mother cells; *e*, functional megaspore mother cell; *f*, male cells; *h*, integument; *n*, nucellus; *q*, body cell nucleus; *p*, prothallus; *r*, resin cavity; *s*, sterile nuclei; *t*, pollen tube; *v*, vascular bundle.

PLATE I

FIG. 1.—Transverse section of mature microsporophyll, showing positions of four microsporangia, resin cavity, and vascular bundle. ×35.

FIG. 2.—Transverse section through micropyle of an ovule about same age as fig. 3; the formation of the "wing" has only just begun. ×205.

FIG. 3.—Median longitudinal section of a young ovule, showing position of megaspore mother cells. ×85.

FIG. 4.—Section through megaspore mother cells in an ovule similar to fig. 3. ×480.

FIG. 5.—Two non-functional megaspore mother cells, showing characteristic appearance of the "brown bodies." ×825.

FIG. 6.—Part of nucellus of an ovule slightly older than fig. 3, showing formation of schizogenous cavities and sliding growth of three cells. ×205.

FIGS. 7, 9.—Megaspore mother cells in synapsis. ×825.

FIG. 8.—Position of mother cell of fig. 7 in relation to surrounding cells. ×205.

FIG. 10.—Sporogenous cells at a somewhat later stage (see text). ×500.

FIG. 11.—Cell 1 of fig. 10. ×825.

FIG. 12.—A functional megaspore and some of the surrounding cells. ×480.

FIG. 13.—A functional megaspore and one of the surrounding cells. ×480.

FIG. 14.—Part of upper cell in fig. 13, more highly magnified. ×1150.

FIG. 15.—A binucleate embryo sac showing disorganization of other sporogenous cells. ×360.

FIG. 16.—A four-nucleate embryo sac and the disorganizing mother cells surrounding it. ×205.

FIG. 17.—Longitudinal section of nucellus, showing position of pollen tube and embryo sac when 64 nuclei are present in the latter; the region occupied by disorganizing spore mother cells is shaded. ×35.

PLATE II

FIG. 18.—Some prothallus nuclei in tangential section of the sac, showing the hollow nucleoli. ×825.

FIGS. 19–21.—Three dividing nuclei in the "alveoli." ×1240.

FIG. 22.—Archegonium initial. ×205.

FIG. 23.—Part of a longitudinal section of a mature prothallus, showing the pollen tube, the basal group of archegonia, and three accessory archegonia; the nuclei of all the basal archegonia are dividing. ×120.

FIG. 23*a*.—The body cell of fig. 23. ×825.

FIG. 24.—Part of one of the archegonia of fig. 23, showing the spindle concerned in cutting off the ventral canal nucleus. ×825.

FIG. 25.—The neck of an archegonium in transverse section. ×205.

FIGS. 26, 27.—Dividing nuclei in the prothallus cells. ×1500.

FIG. 28.—Mature archegonium; the position of the pollen tube is indicated above the neck. ×360.

FIG. 29.—Young pollen tube; only a single nucleus is present. ×480.

FIG. 30.—Tip of young pollen tube showing three nuclei. ×825.

FIG. 31.—Part of nucellus, showing position of the tube of fig. 30. ×50.

Fig. 32.—Young pollen tube with body cell and two sterile nuclei; the position of this tube is shown in fig. 17. ×825.

PLATE III

FIG. 33.—Tip of pollen tube just entering the prothallus. ×205.

FIG. 34.—Tip of pollen tube after growth of the tube has ceased; the sterile nuclei with their surrounding cytoplasm form a distinct cell; a small fragment of the body cell nucleus has separated off. ×205.

FIG. 35.—The body cell nucleus of fig. 34. ×825.

FIG. 36.—Tip of mature pollen tube, showing position of male cells and the relation of archegonia to the pollen tube. ×205.

FIG. 37.—Male cells of fig. 36. ×480.

FIG. 38.—Part of a transverse section of a prothallus, showing an archegonium containing two free nuclei, the daughter nuclei of the oospore. ×360.

FIG. 39.—Diagrammatic longitudinal section of proembryo with five nuclei; reconstructed from serial sections. ×170.

FIG. 40.—Similar section of proembryo with ten nuclei; reconstructed from serial sections. ×230.

FIG. 41.—One of the sections from which fig. 39 was constructed, slightly oblique, showing the upper four nuclei and the cleavage planes (?) between them. ×200.

FIG. 42.—Young seedling. ×1.5.

FIG. 43.—Cotyledons of same. ×3.7.

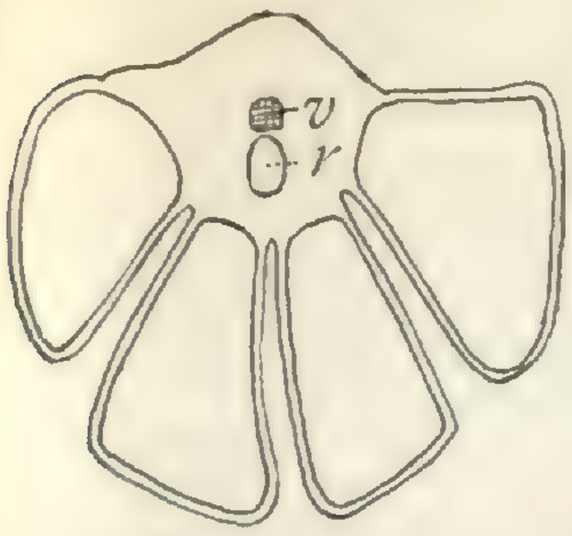
FIG. 44.—Abnormal pollen tube (see text). ×50.

FIGS. 44*a*, *b*.—Nuclei of fig. 44. ×205.

FIG. 45.—Abnormal archegonium. ×205.

FIG. 45*a*.—Part of fig. 45 (see text). ×825.

FIGS. 46*a*, *b*.—Two adjacent sections of the nucleus of an abnormal archegonium. ×825.



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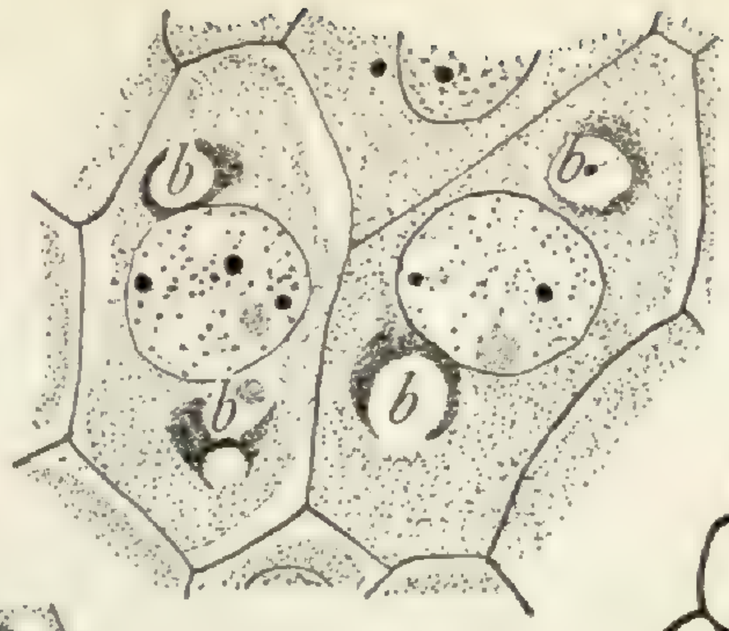

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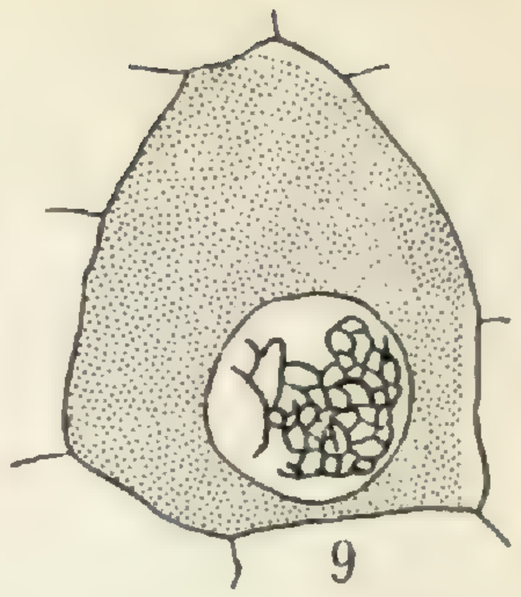

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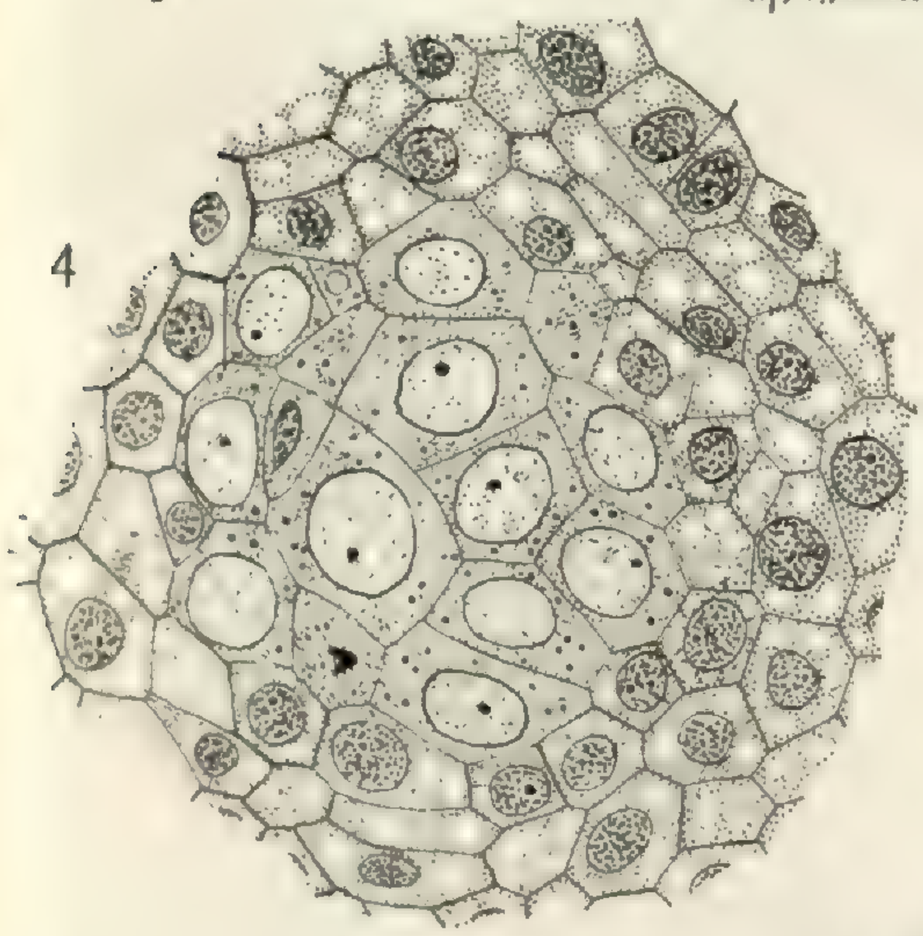

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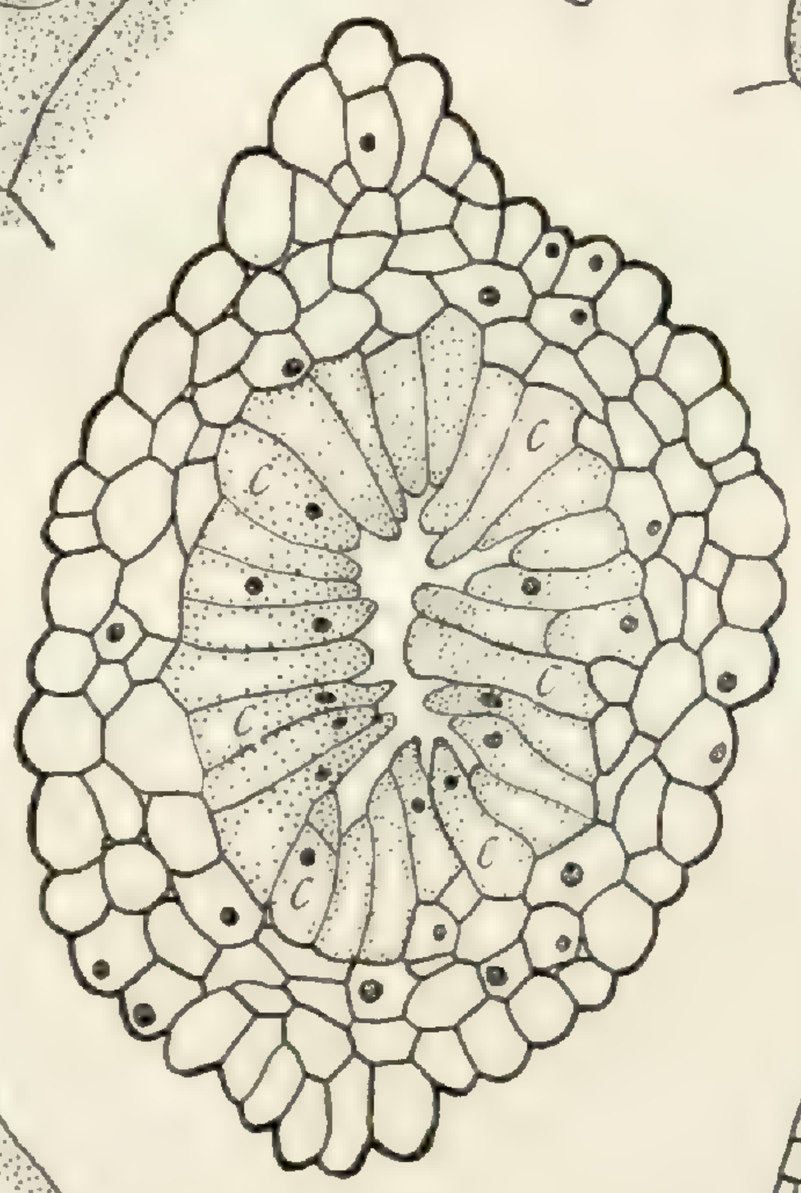

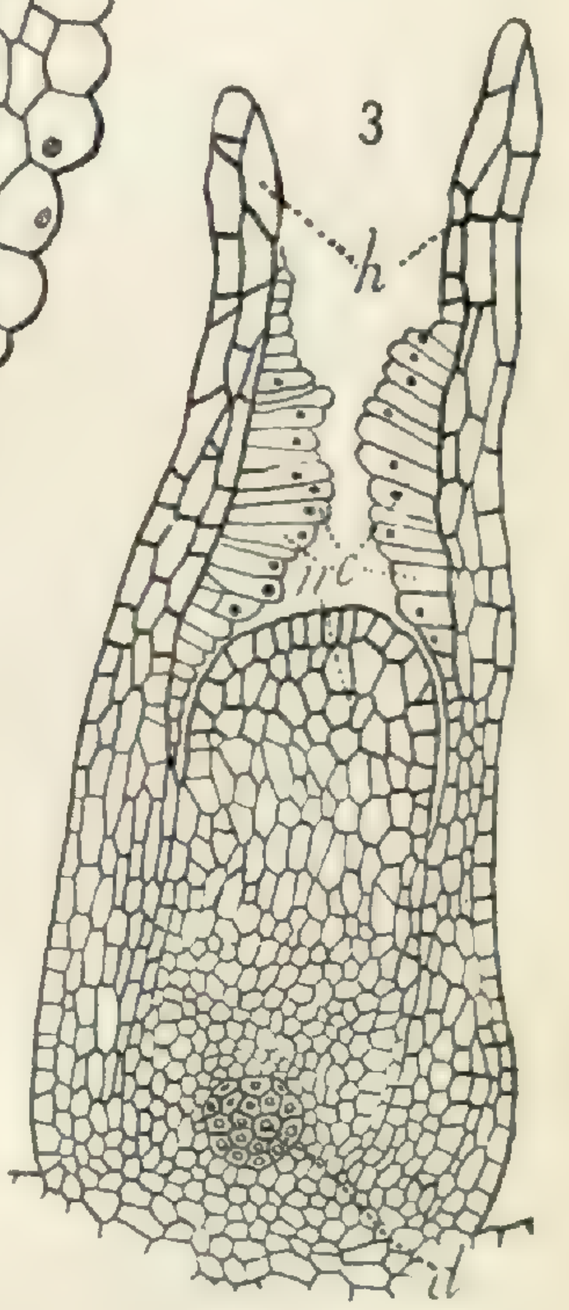

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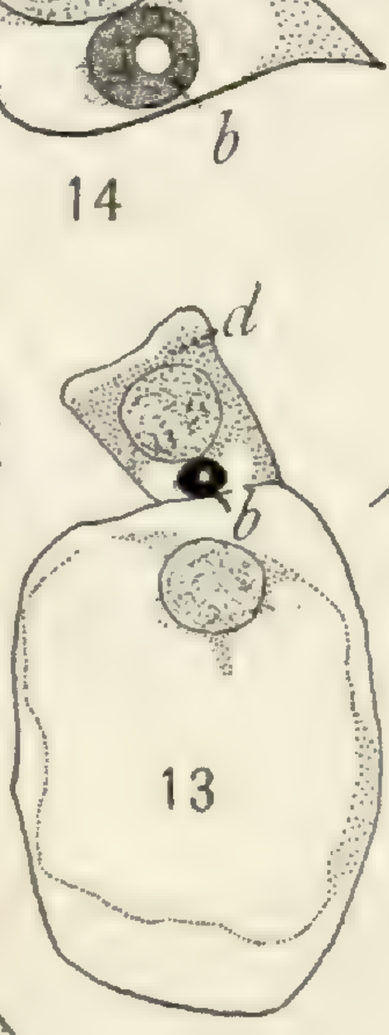

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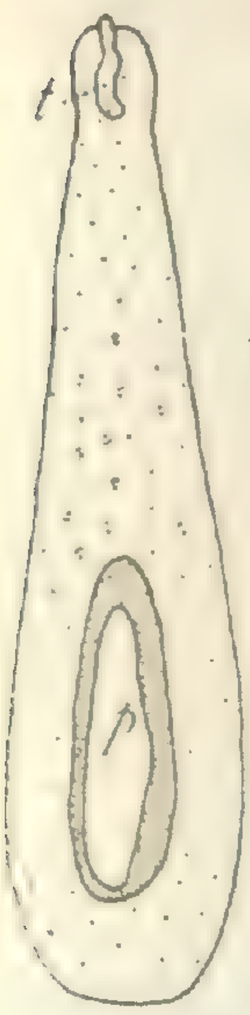

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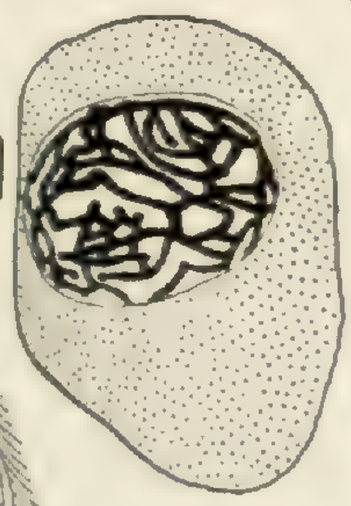

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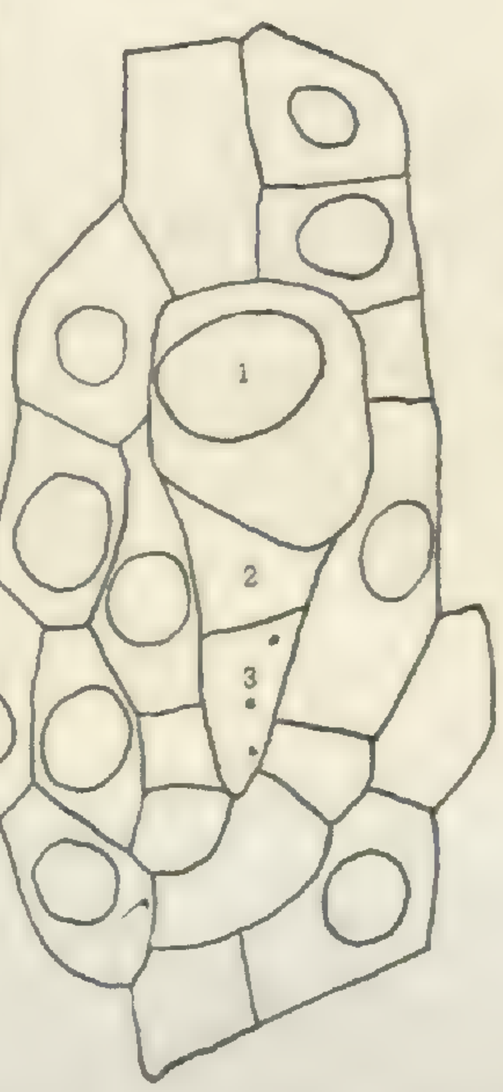

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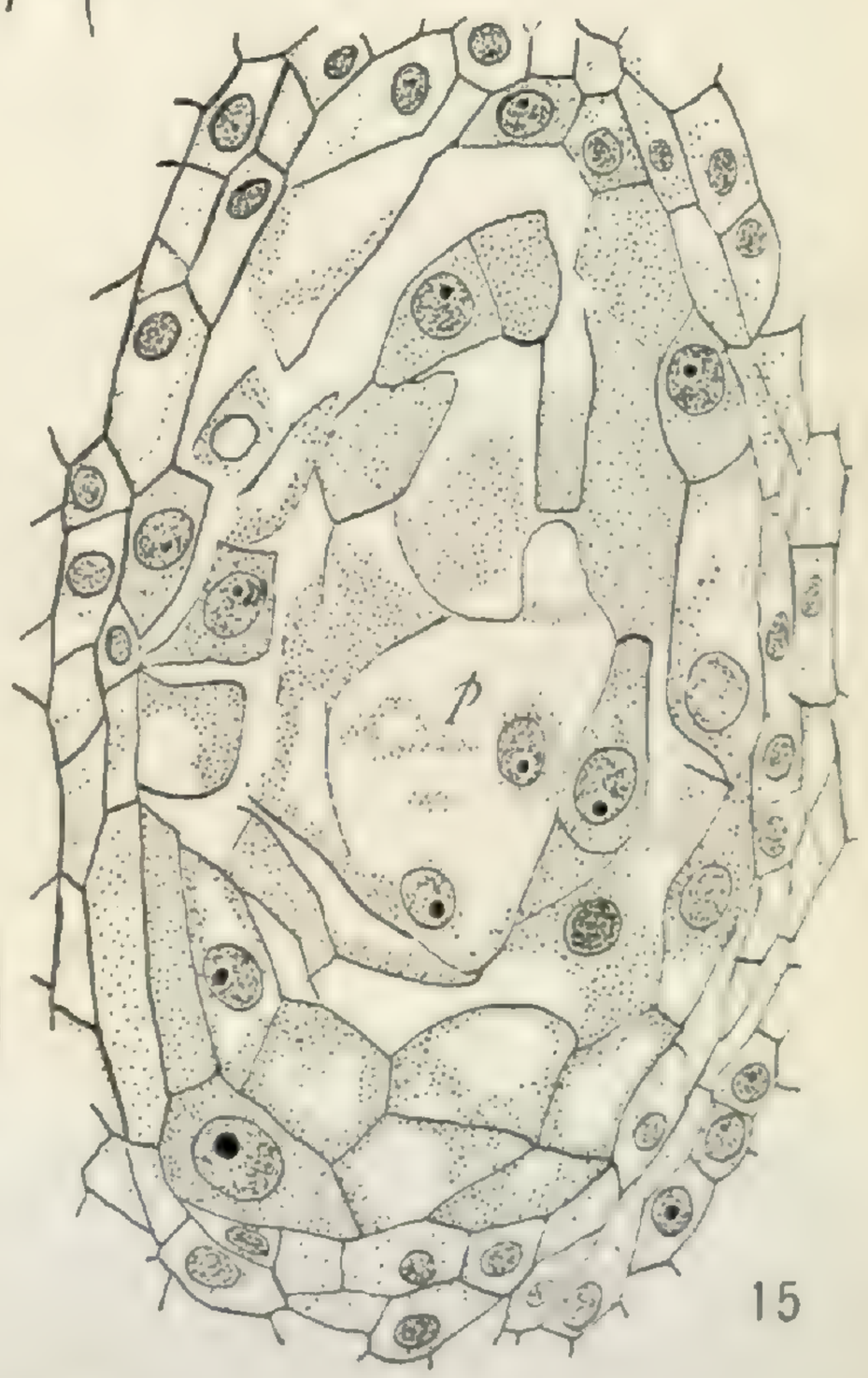

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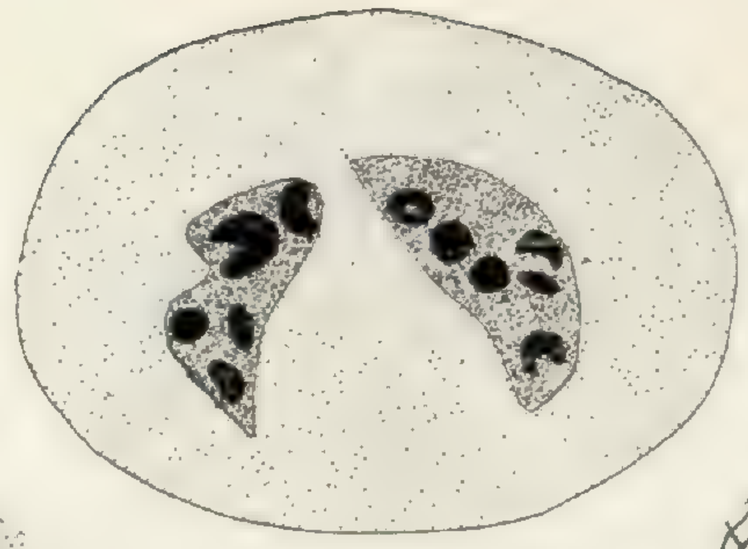
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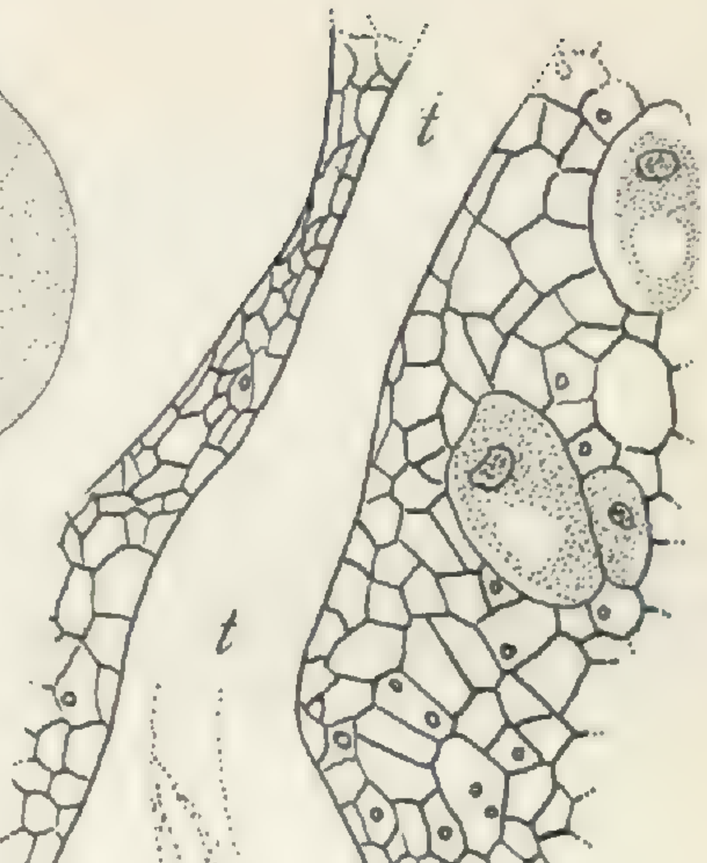
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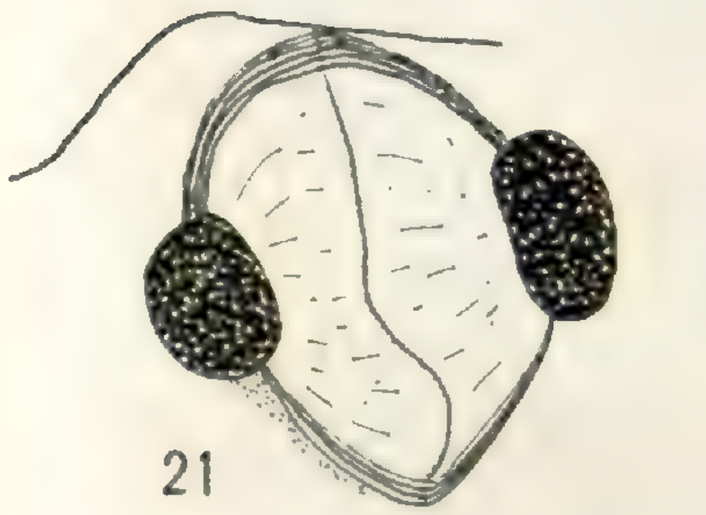
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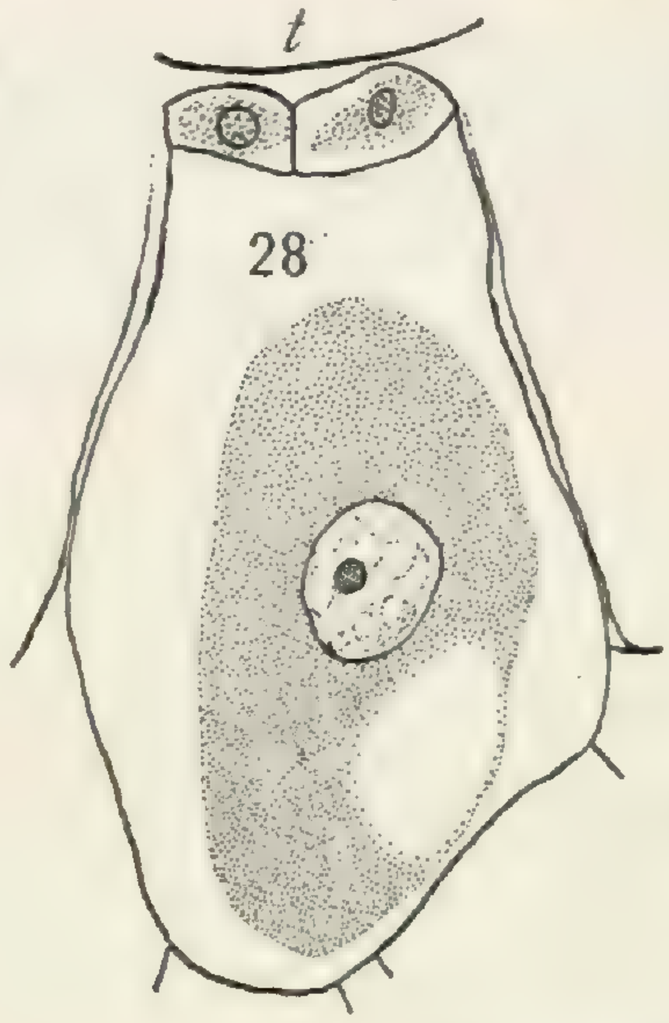
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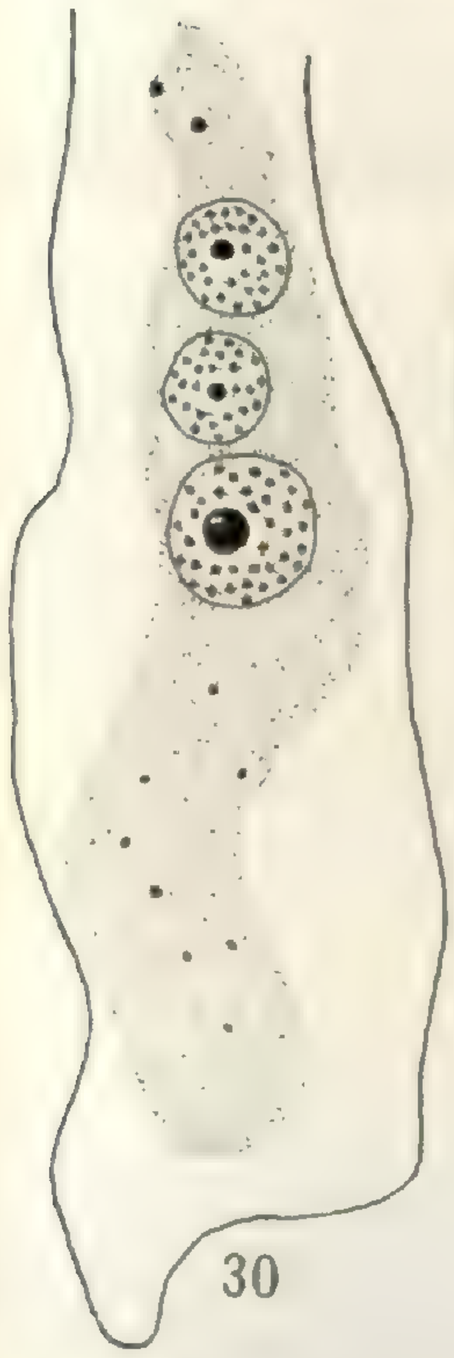
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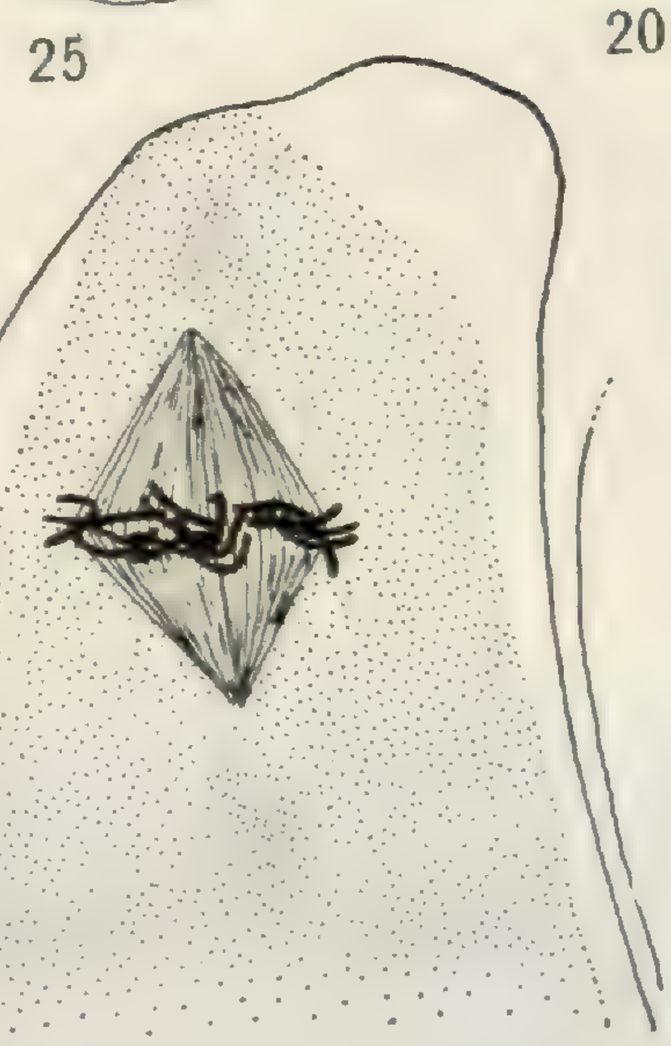
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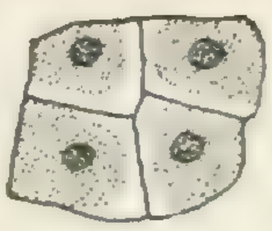
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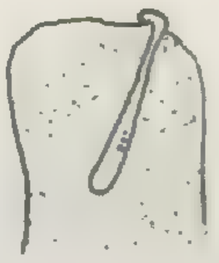
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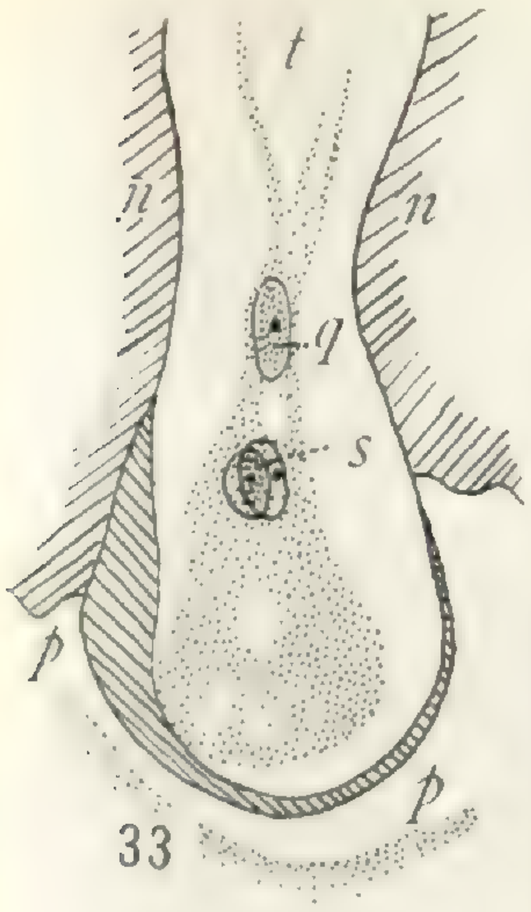
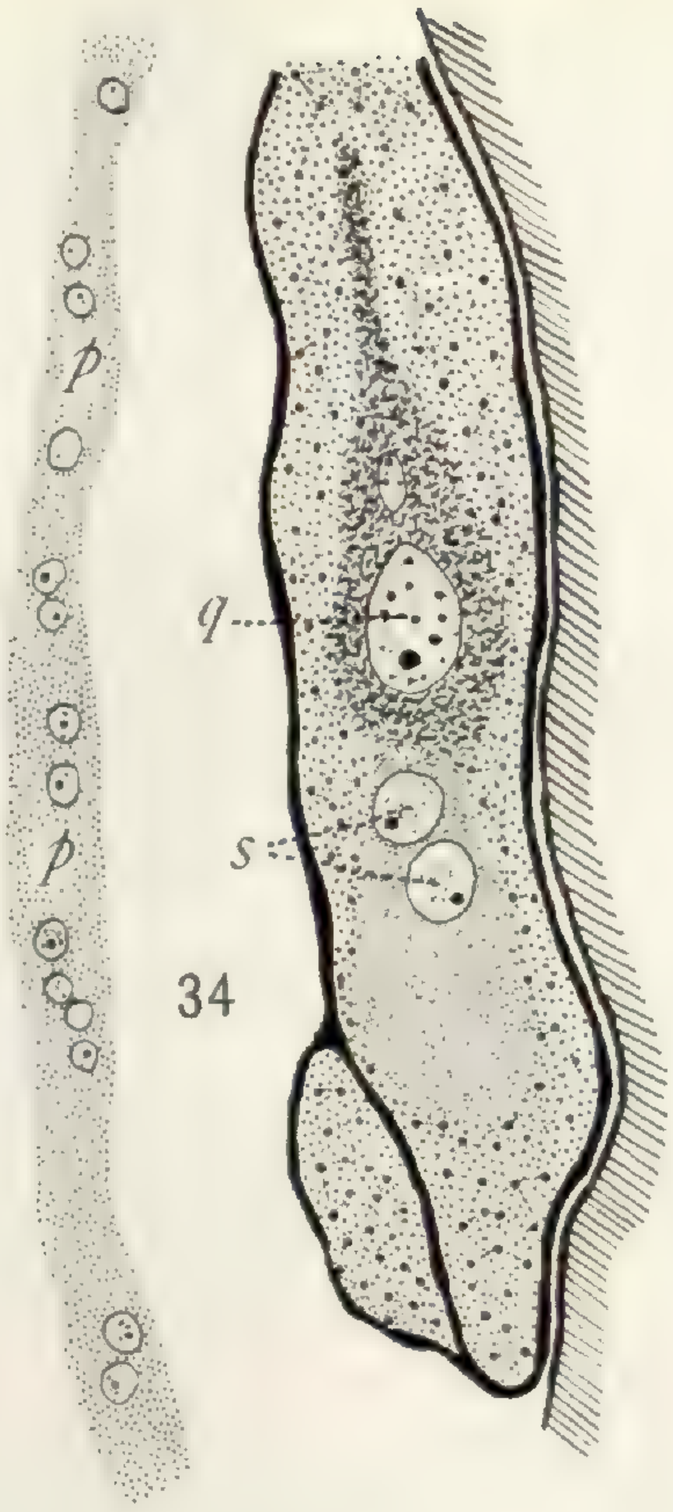
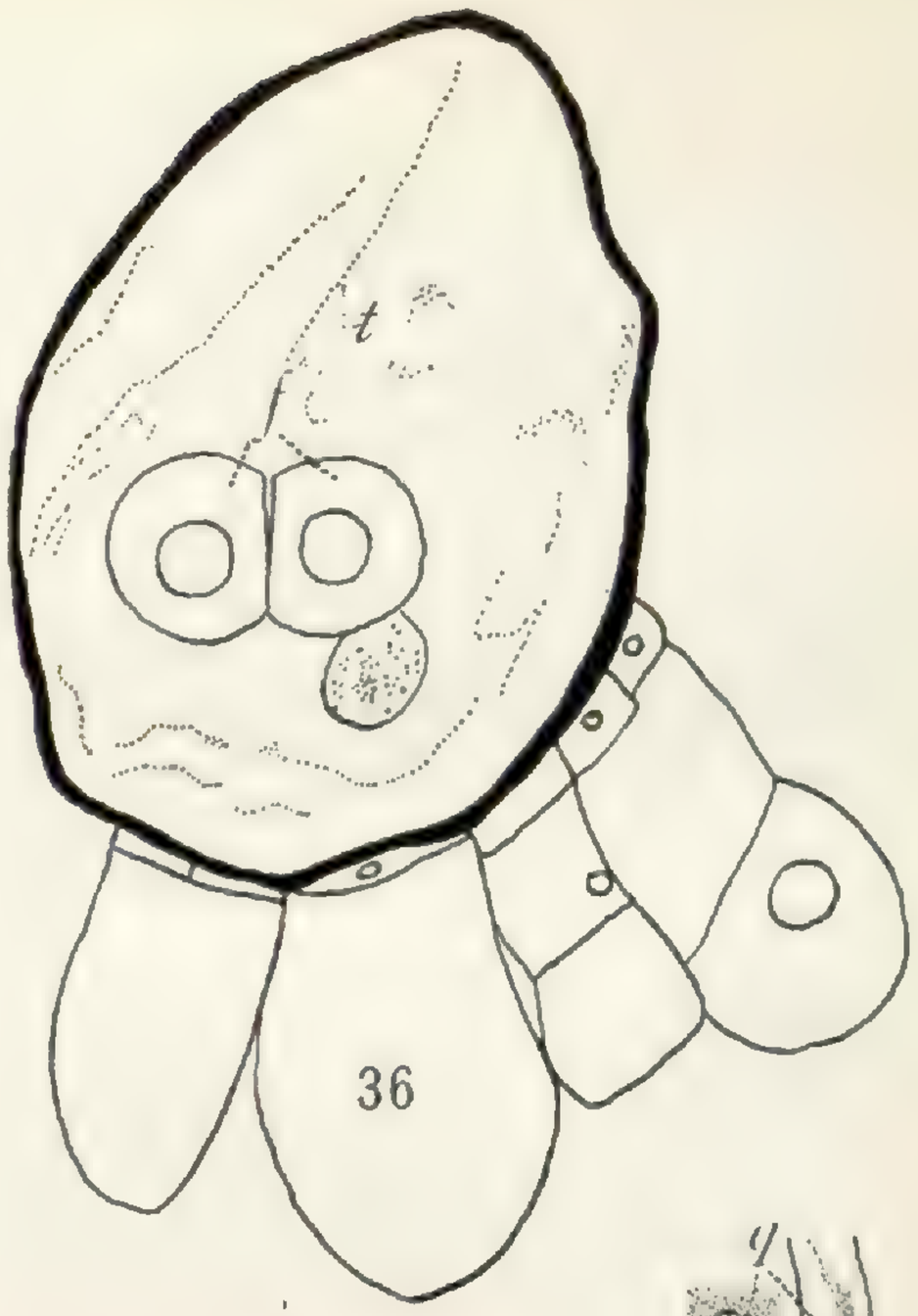
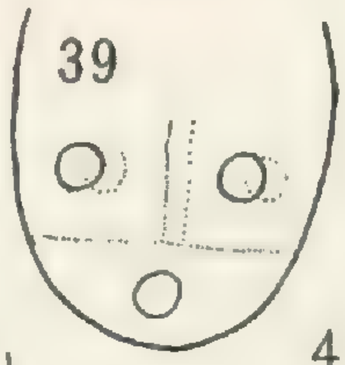
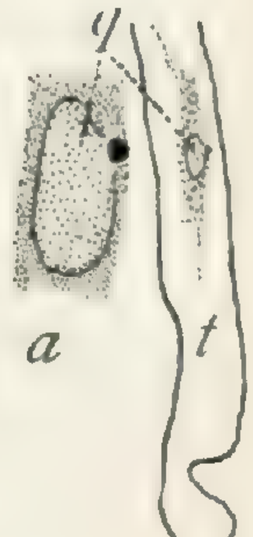
SAXTON on WIDDRINGTONIA

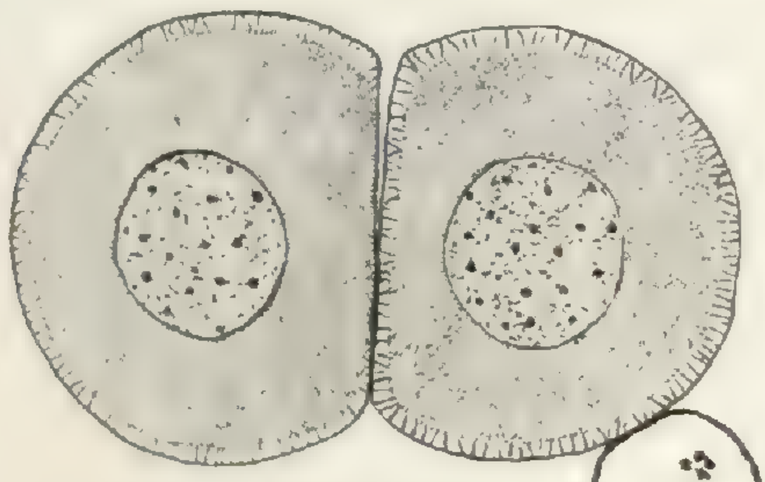


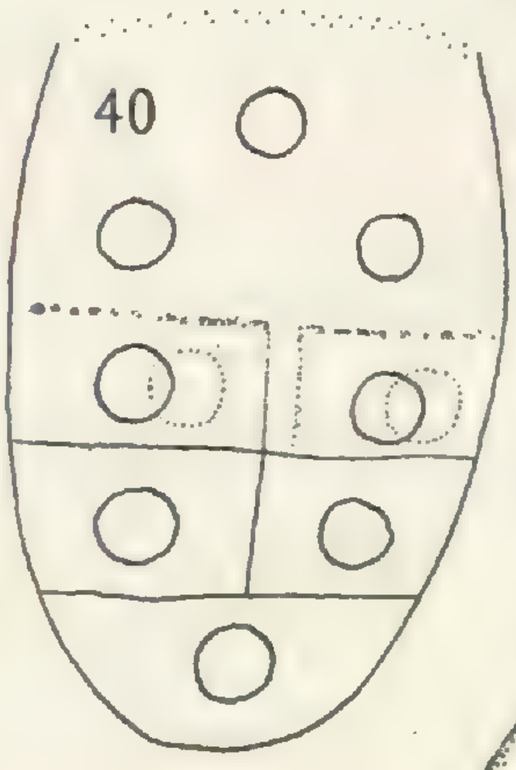


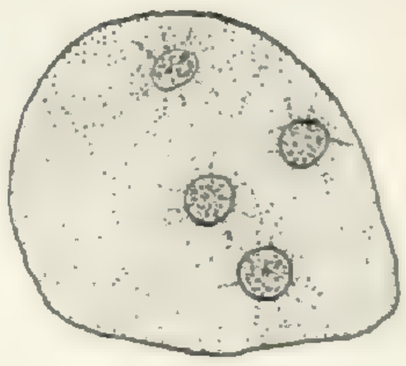


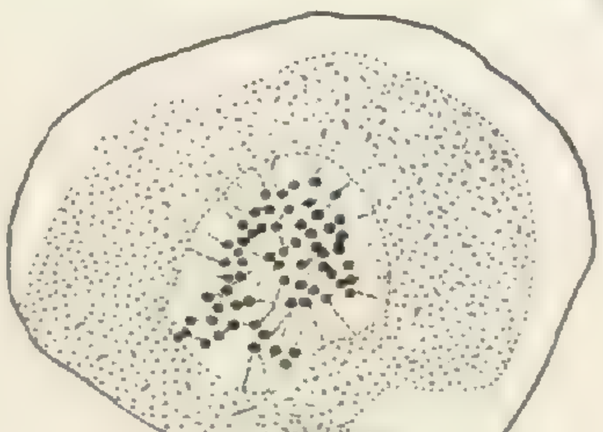


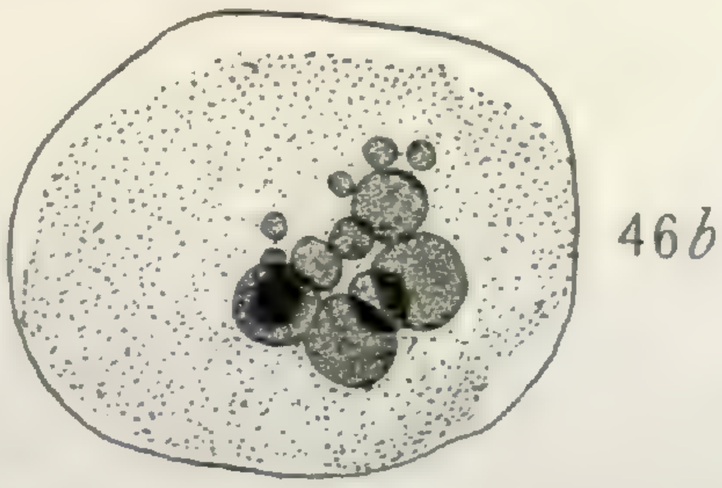


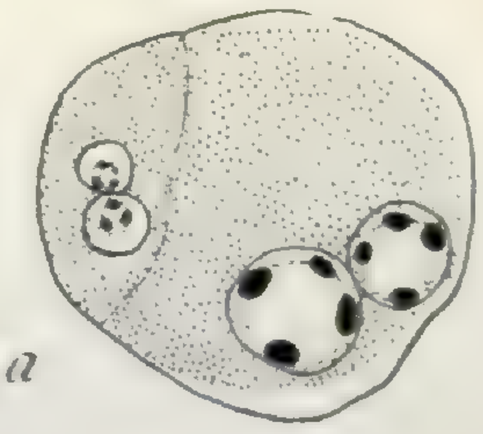












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SAXTON on WIDDRINGTONIA

SOME PECULIAR FERN PROTHALLIA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 137

LULA PACE

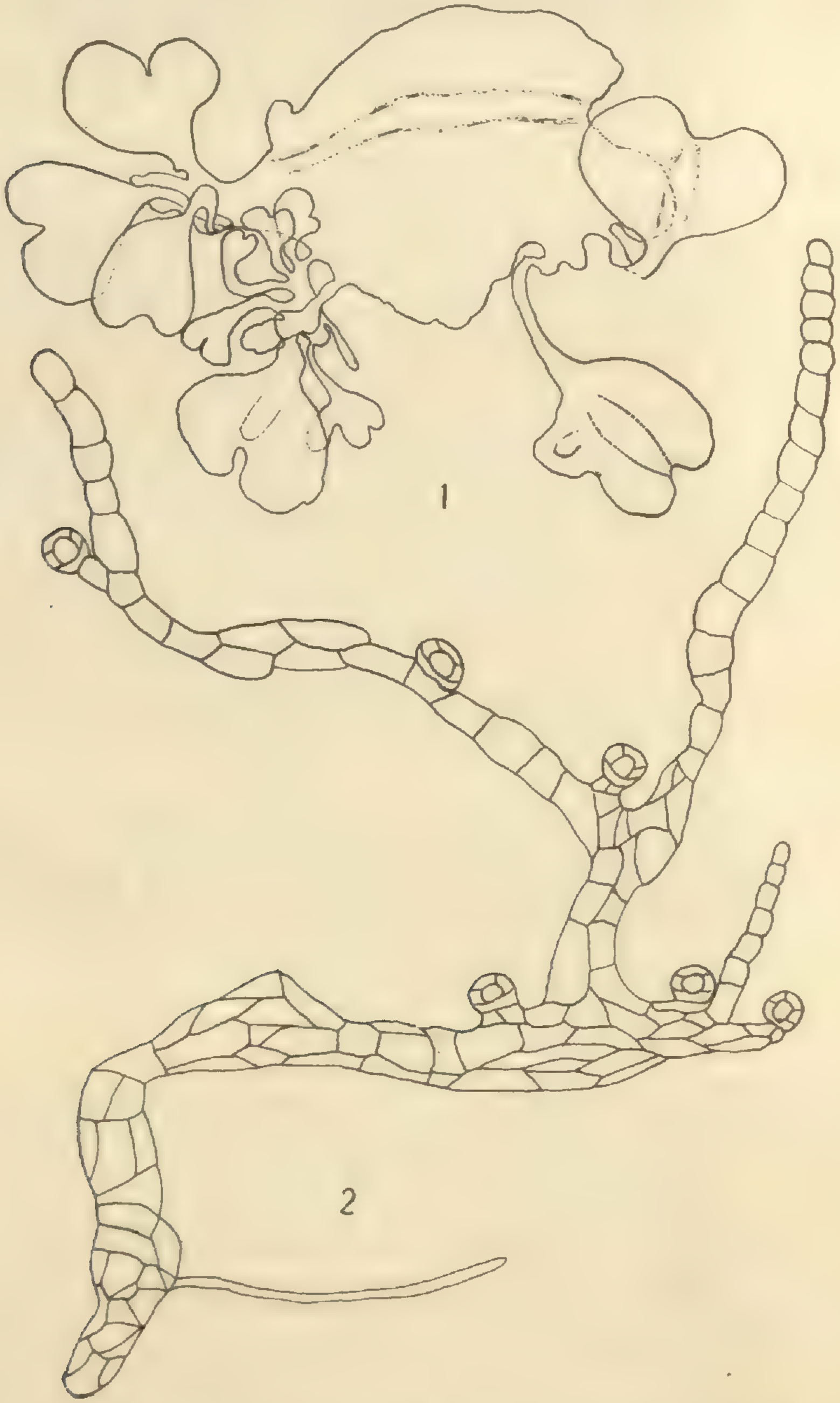
(WITH ELEVEN FIGURES)

In September 1906 Miss S. M. HAGUE sent me some fern prothallia from a swamp in northern Indiana, where they were growing luxuriantly on rotten wood. Pieces of the wood were put into a glass jar, which was covered and placed on a table about seven feet from a window with a southeast exposure. They were kept very moist, yet watered with care, so as not to allow any water to get on the plants and thus cause fertilization. In spite of this precaution, however, enough moisture probably collected on the plants to permit fertilization occasionally, for sporophytes developed at intervals. Some of these, as well as many of the gametophytes, were used in class work. A few of the sporophytes are about 7 cm. high. They resemble SLOSSON'S figures of *Dryopteris spinulosa intermedia* (*Aspidium intermedium* Muhl.). Certain peculiarities found in this material seem worth describing. Some of the gametophytes are still growing and will be watched for further developments.

Gametophytes

The prothallia were of the typical heart-shaped form, the larger ones being about 5 mm. long. Those on which sporophytes have not developed have continued to grow, and many spores, which had been lying for a long time in the rotton wood, have germinated. The old prothallia have grown to unusual size and taken queer shapes, many of them being 15 mm. long, a few 23 mm., and one even measuring 37 mm. The most striking thing about them, however, is the peculiar forms developed. A hasty observation of one of these often gives the impression of a number of prothallia near together and overlapping, for they often branch, apparently from any part of the plant, as in fig. 1, which is a diagram of one of the simpler cases. At one point near the margin of another plant 21 of these branches were counted, all 1–1.5 mm. long, and each bearing 6–10 antheridia. In

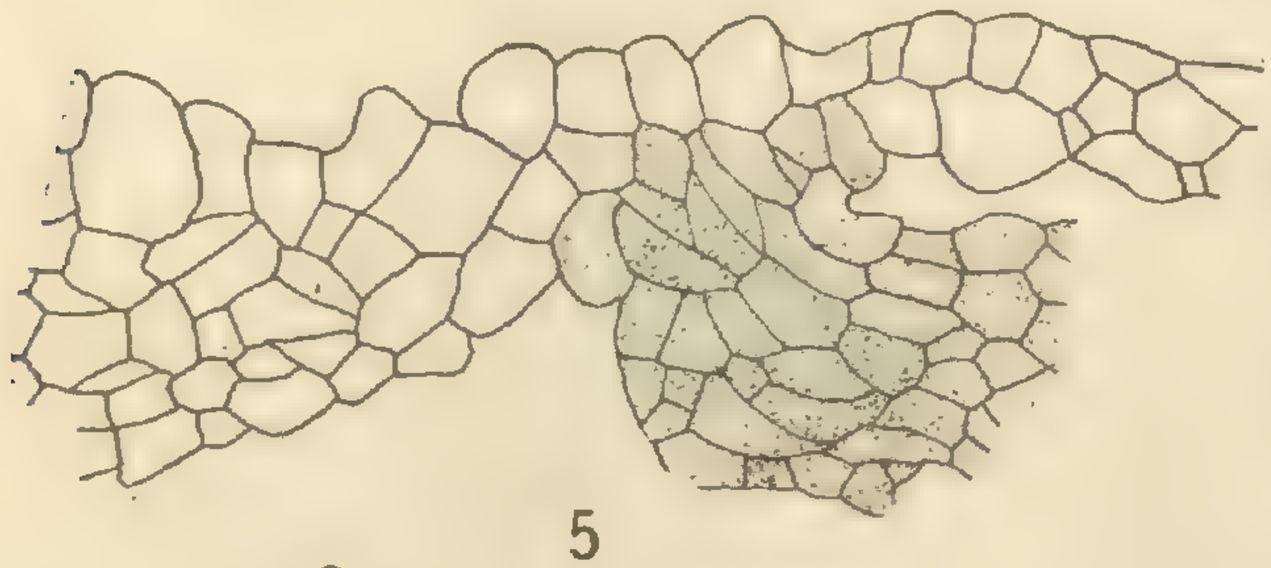
some cases filamentous processes grow out (fig. 2); this figure was made from fresh material, and the cell walls may not be accurate in



FIGS. 1, 2.—Fig. 1, diagram of one of the simpler prothallia with several gametophytic branches; fig. 2, sketch of a filamentous process with antheridia, from living material.

every case. Occasionally a cylindrical process was seen, as described by LANG (2), but it might possibly have developed into the ordinary form, for some of the branches have slender bases. In several

instances this outgrowth is from the apical region, as shown in the diagram (fig. 3), which represents a small prothallium 5 mm. long. The outgrowth has antheridia along the margins, but shows no archegonia; these were present, however, on the main prothallium.



FIGS. 3–6.—Fig. 3, prothallium 5 mm. long, with apical process bearing antheridia but no archegonia, which are found on the main prothallium; fig. 4, section through a very young gametophytic branch with apical cell; the branch is at the edge of the section and near an archegonium, the cross-section of the neck of which is shown; fig. 5, section through the basal part of a gametophytic branch, showing its relation to the main gametophyte; fig. 6, an antheridial prothallium 23 mm. long, with many archegonia but no antheridia except in the basal region.

Sections of this prothallium show nothing unusual in structure or cell contents.

A section of one of these branches at a very early stage shows its relation to the main prothallium (fig. 4). It comes from the edge of the archegonial cushion, the section showing also the neck of an adjacent archegonium. So far as the apical region is concerned, it

looks like a normal gametophyte. The basal part of a somewhat older branch is shown in fig. 5, which is broader and does not seem so closely related to archegonia, although near the cushion. Apparently any cell or group of cells may be rejuvenated and initiate this branching. The cells in the neighborhood of fig. 4 are very large for cells in a position so near the apical region, and they contain unusually large food bodies, apparently oil globules; this may be a condition that leads to branching.

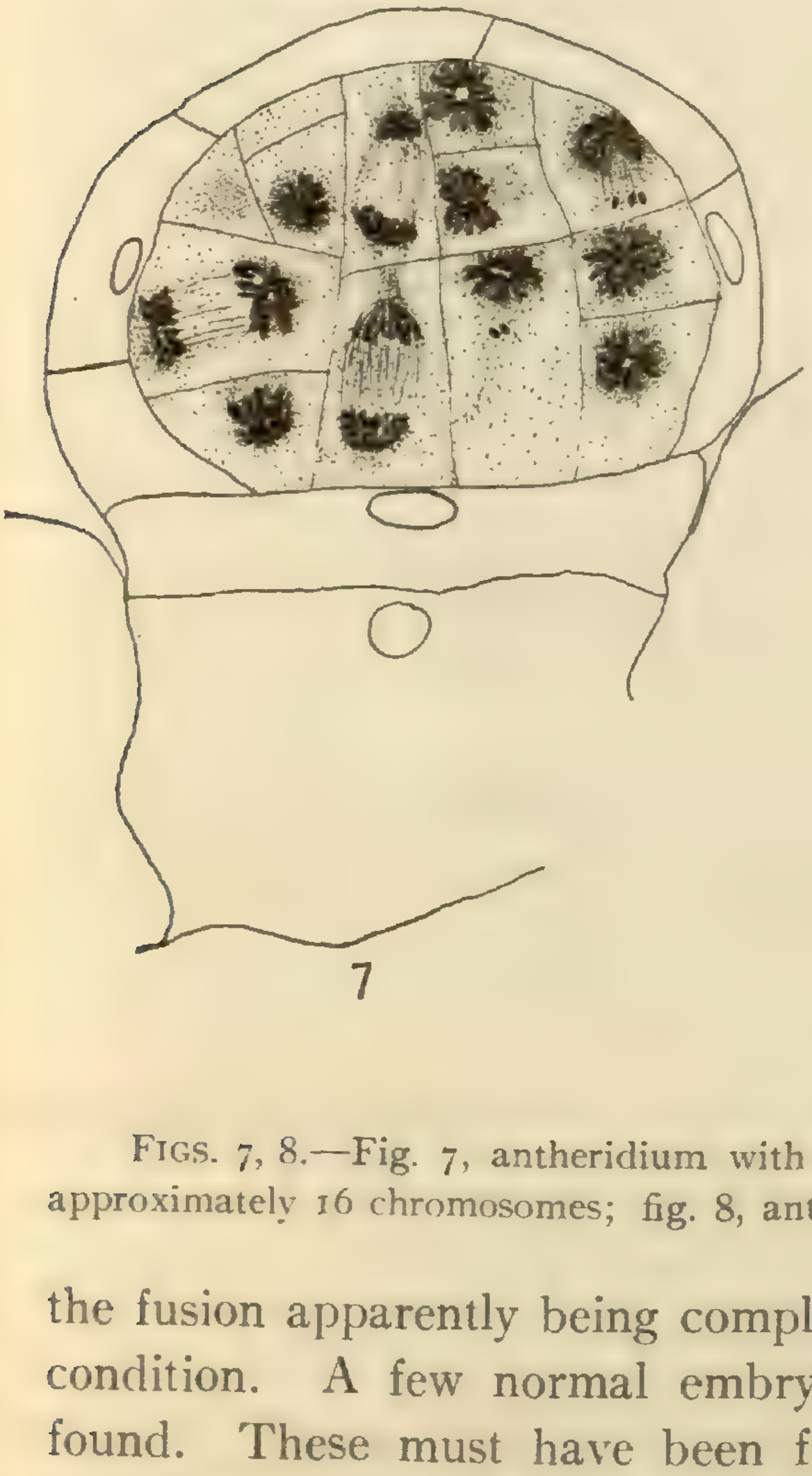
Another type of gametophyte is shown in fig. 6. This prothallium does not branch and is 23 mm. long. There are few or no antheridia on prothallia of this type except near the basal region, but the archegonial cushion is unusually wide and thick, and has a broad row of archegonia along both margins, with more in the center. Transversely, these rows have 1–5 archegonia very closely crowded together. In one gametophyte 16 mm. long, there were found by actual count 142 archegonia on one side of the cushion, with apparently as many on the other side; so that instead of the usual small number of archegonia, there were probably not far from 300 on this particular gametophyte, and other gametophytes of this type. The production of archegonia apparently goes on indefinitely, for the prothallia still looked vigorous.

Antheridia and archegonia

A rather complete series of stages in the development of antheridia and archegonia was examined, but most of them resembled the usual type. Two late antheridial stages are shown in figs. 7 and 8, the former with the spermatogenous cells in mitosis, and the latter with sperms almost mature. There are apparently 16 chromosomes, though none of the figures are in condition to permit absolute accuracy in counting. As a rule, antheridia are found only on the basal region of old prothallia or on the branches, but occasionally one or two appear at any point on the gametophyte. In a few instances immature antheridia were found among mature archegonia. An unexpected feature in archegonial development is their appearance far back from the growing point, so that young archegonia are found among the old ones. A peculiarity several times noted was two archegonia with no wall between the egg cells, but with two complete necks; otherwise nothing unusual was seen in their development.

Fertilization

A few prothallia were placed in water for a short time, and fertilization took place in the usual way, one or more sperms entering the neck and reaching the so-called receptive spot, where one sperm enters the egg. The sperm nucleus fuses slowly with the egg nucleus,



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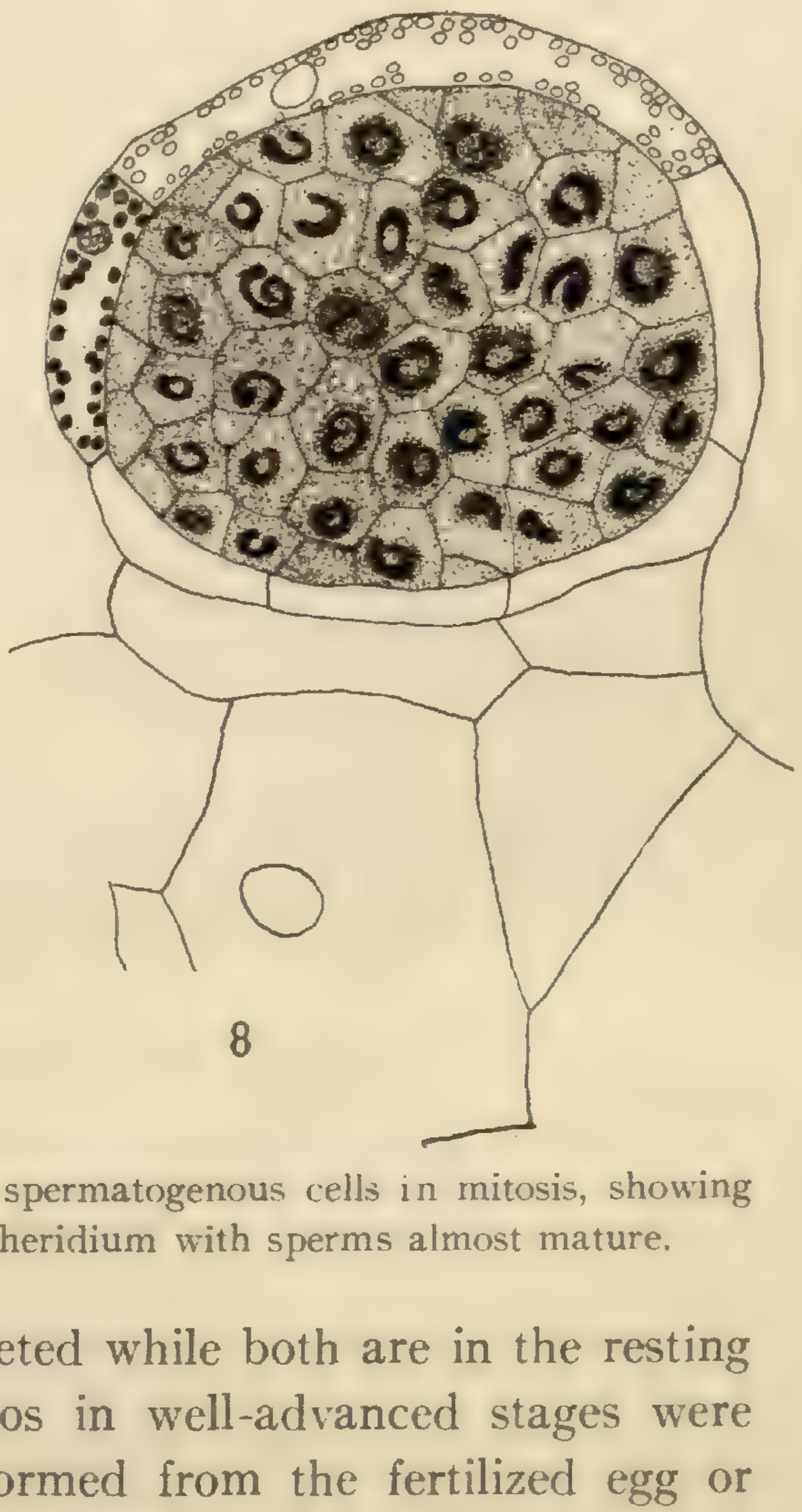

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FIGS. 7, 8.—Fig. 7, antheridium with spermatogenous cells in mitosis, showing approximately 16 chromosomes; fig. 8, antheridium with sperms almost mature.

the fusion apparently being completed while both are in the resting condition. A few normal embryos in well-advanced stages were found. These must have been formed from the fertilized egg or have been developed parthenogenetically.

Apogamy

A peculiar structure was found on the gametophyte which bore the antheridia shown in fig. 8, but it was found on the upper surface. The diagram (fig. 10) shows the relation of this body and the antheridium to each other and to the archegonia. It is clear that there are only two possible interpretations of this structure: it must be an

abnormal antheridium, or it is a sporangium; if it is the latter, this is a case of apogamy. The great difference in size is seen by com-

FIGS. 9, 10.—Fig. 9, a sporangium-like structure from the upper surface of the gametophyte from which was drawn fig. 8; two layers of cells outside the fertile region, the inner layer suggesting a tapetum; each layer consists of many cells; fig. 10, diagram showing the relation of figs. 8 and 6 to one another and to the archegonial region.

paring the figures, which are drawn to the same scale. Among all the antheridia examined from this material, there is no such difference in size, the antheridium shown in fig. 8 being a rather large one. In

all the antheridia only one layer of wall cells is present, and these are few and rather definitely placed. But this structure shows two distinct layers (figs. 9, 10), except in one section, and this at only one place (fig. 11). Here for the space of two cells the wall is only one cell thick, but these two cells might divide and make the two layers complete. The outer layer consists of many cells, which always contain chloroplasts, but the next layer contains chloroplasts in a few cells only. The nuclei in this second layer are quite different from those in the interior, and in some of the cells there is a suggestion of the usual tapetal appearance. It does not have the long slender stalk characteristic of the normal sporangia of the higher Polypodiaceae, but it probably would have elongated somewhat before maturity, making it very similar to the stalks of the Osmundaceae. Consequently, this structure is quite unlike an antheridium, and is almost perfect in its sporangial characters. As there were no mitotic figures, it could not be determined whether the nuclei contained the sporophytic or gametophytic number of chromosomes, but we should expect

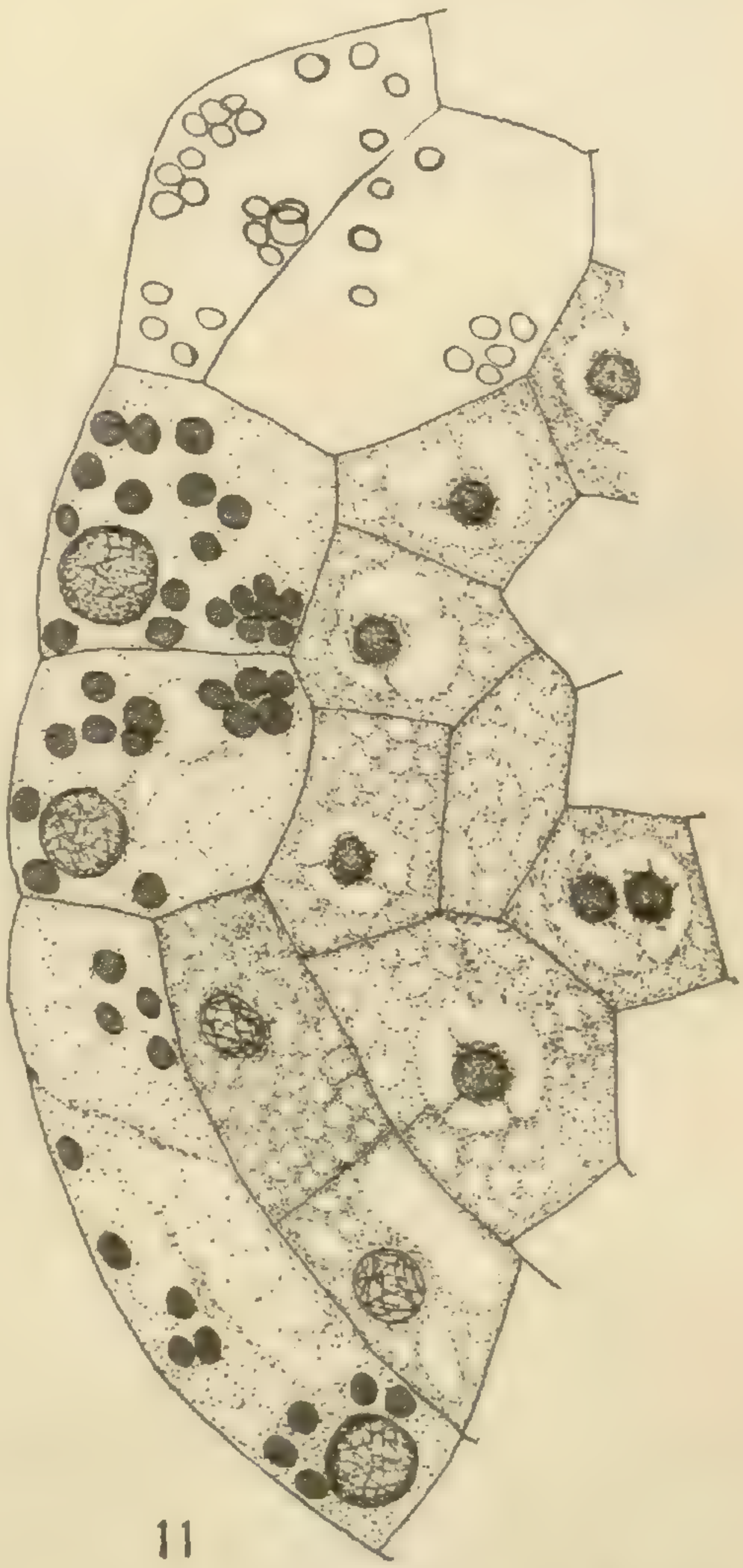

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FIG. 11.—A small portion of the same sporangium-like structure shown in fig. 9, but from another section; this is the only place where one layer of cells appears outside the fertile region, and these two cells might divide and make the two layers complete.

the sporophytic number to appear, especially since another prothallium bore a mature sporangium of the *Osmunda*, type, with a few spores still remaining in the sporangium. In the absence of mitotic figures, such a sporangium easily invites speculation. It

may be an x structure, and the spores may have been formed in the usual way, so that the new gametophyte will have only $\frac{1}{2}x$ chromosomes; an interesting surmise in view of the fact that nearly related forms are known to show 12, 24, and 48 chromosomes. Or there may have been a doubling of the number and a subsequent reduction at the formation of spores. The appearance of a sporangium upon a prothallium will be accepted as a case of apogamy.

Discussion

LANG (**2**), in his work on apogamy, grew prothallia from spores. Such prothallia, when kept dry, in direct sunlight, and watered only from below, developed leaves, roots, and ramenta on the prothallia themselves or on the cylindrical processes. The process continued as a leaf, or it produced sporangia, and tracheids were found both in the process and in other parts of the prothallium. When sporangia were found on a cylindrical process, tracheids were always present in the underlying tissue. YAMANOUCHI (**7**) reports very slow growth and few abortive archegonia in his material kept in bright light and dry air.

My material was not in bright light and was given plenty of moisture, being kept in as nearly normal condition as possible, except for the entire absence of liquid water. Consequently, if this is apogamy, the lack of fertilization is apparently the only factor involved in its appearance here, for in this material archegonia were very numerous and were normal in every respect, and fertilization did take place when water was supplied. In this respect it seems to be like *Marsilea*, where SHAW (**3**) and STRASBURGER (**5**) found that if megaspores of *Marsilea Drummondii* were isolated, and therefore fertilization prevented, parthenogenetic (apogamous) embryos were produced.

The gametophyte number of chromosomes is approximately 16. This number is very suggestive of Osmundaceae (SMITH **4**, STRASBURGER **6**, YAMANOUCHI **8**), which is reported to have 16 chromosomes in the spore mother cell. However, the young sporophyte does not resemble the mature form of *Osmunda*, and whether it resembles the sporeling I cannot tell, not being familiar with the sporelings of *Osmunda*.

The sporophyte structures afforded no opportunity for determining whether it contained the haploid or diploid number of chromosomes. YAMANOUCHI found the haploid number of chromosomes in apogamous embryos, and concluded that the number of chromosomes is not the only factor which determines the characters of the sporophyte and gametophyte. STRASBURGER (**5**) found two kinds of megaspores in *Marsilea Drummondii*, some with the haploid and some with the diploid number of chromosomes. It would be expected that those with the diploid number of chromosomes would develop sporophytes without fertilization, as the gametophyte, and consequently the egg, has the diploid number already present. FARMER and DIGBY (**1**) found a vegetative fusion of nuclei in two forms, thus getting the sporophytic number of chromosomes without ordinary fertilization.

The question of apogamy and the literature on the subject will not be discussed further at present, as it is hoped the material may furnish further evidence of this condition.

It is a pleasure to express my obligations to Dr. CHARLES J. CHAMBERLAIN for advice and criticism during this work.

Summary

Prothallia kept for three years in the laboratory in as nearly normal conditions as possible, except for the absence of liquid water, continue to grow, but develop peculiar forms and branching of various types.

The sex organs continue to develop, antheridia being found occasionally on the main plant in all positions, but especially on the branches. Archegonia become very numerous, approximately 300 having been found on one gametophyte. These not only develop in the apical region, but also far back among the old archegonia.

Fertilization may take place whenever liquid water is present, as shown in several cases where gametophytes were placed in water and sectioned later.

Apogamy is present in a sporangium-like structure which lacked the long stalk of the Polypodiaceae, but was not unlike the younger stages of the sporangium of the Osmundaceae. It had two layers of cells outside the fertile region, the inner of these layers resembling a tapetum.

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PERIODICITY IN DICTYOTA AT NAPLES

I. F. LEWIS

(WITH ONE FIGURE)

Periodicity in the production of the sexual cells of *Dictyota dichotoma* has been described by WILLIAMS (**8**) for Bangor, Wales, and Plymouth, and by HOYT (**2**) for Beaufort, North Carolina. At Bangor the sexual products are liberated at fortnightly intervals, the rudiments of sexual organs appearing a few tides before the least neap, and the mature gametes being liberated 3–5 tides after the greatest spring. In October, however, the time relations are reversed. At Plymouth the crops are later, as well as slower in maturing, than at Bangor, liberation occurring 7–12 tides after the greatest spring. At Beaufort only one crop a month is produced, the initiation of rudiments occurring the day before, or the day of, and liberation taking place six days after, the greatest spring tide.

These striking differences in the behavior of what is pronounced to be the same species in different localities make it desirable that careful observations be recorded for this form in other regions than those mentioned, and especially in those regions where the tidal relations are different. WILLIAMS surmises that "the periodicity of the sexual cells is an hereditary character, and consequently may be expected to manifest itself in seas and habitats where there are no tides." OLTMANS (**5**, pp. 487, 488) states: "WILLIAMS findet einen Zuzammenhang der Entwickelung und Befruchtung und mit den bekanntlich in Abständen von 14 Tagen auftretenden 'Spring- und Nipptiden.' Da solche im Mittelmeer fehlen, werden erneute Untersuchungen hier die Dinge zu klären haben."

With these facts in mind, I took occasion, during March and April 1908, to make daily notes on the condition of the sexual plants of *Dictyota* at Naples.[1] The results of these observations are here presented.

[1] I take this opportunity of expressing my thanks to the directors of the Smithsonian Institution for the privilege of occupying a table at the Zoological Station in Naples, and to Dr. R. DOHRN and Dr. LO BIANCO for their cordial cooperation during my stay in Naples.

The range of the tides at Naples is very much less than at either Beaufort or Bangor, though it cannot be said that tides are wholly lacking at this point. The daily readings of the tide gauge near Naples, furnished by the Italian government, agree closely with the tides predicted by the U.S. Coast and Geodetic Survey. Extraordinary conditions of wind and weather, however, may affect the range of the tides very appreciably. For the period studied, the maximum daily range of the tides was 2.1 feet, the minimum 0.4, the average 1.0. The water level varied from 0.7 feet below to 1.5 feet above mean low water of spring tides. The following table gives an idea of the relative ranges of the tides at Bangor, Beaufort, and Naples.

TABLE I

	Average range	Difference in height of low water at spring and neap tides
Bangor	17.9 feet	5.7 feet
Beaufort	2.8	0.5
Naples	1.0	0.25

The sexual cells of *Dictyota* were found to be produced at regular intervals, the time of initiation of the rudiments and liberation of the mature gametes bearing a definite relation to the periodic changes in the tides. The crops are borne, as at Bangor, at fortnightly intervals. Initiation of the rudiments occurs on the same day as general liberation of the mature gametes, this being two or three days after the least neap tide. The number of days required for the development of a single crop is approximately sixteen. The development of the sori is fairly uniform, not being accelerated at the time of the spring tides.

A comparison of the facts of periodicity in *Dictyota* at Bangor, Beaufort, and Naples is given in the following tables.

The accompanying chart (fig. 1) gives in graphical form the record of one crop from initiation to liberation, showing the relations between the tidal changes and the fructification of *Dictyota*. The chart should be compared with the charts given by HOYT (**2**, pp. 386, 387) in order to compare the behavior of *Dictyota* at various localities.

At any given time all the individual plants, collected at various points from Capo Miseno to Santa Lucia, are at approximately the same stage of development. There are noticeable differences, however, as for instance in the plants collected on April 10. According to the chart, this date shows the beginning of liberation of gametes,

TABLE II

	Initiation	Liberation	Time of development
Bangor	A few days before the the least neap	3–5 tides after greatest spring	12–17 days
Beaufort	Day before or day of greatest spring	6 days after greatest spring	8–9 days
Naples	2–3 days after least neap	2–3 days after least neap	16 days

TABLE III

HISTORY OF A SINGLE CROP

Day	Beaufort	Bangor	Naples
1	Undivided rudiments	Undivided rudiments	Undivided rudiments
3	8–16 cells in surface view of antheridia	Undivided rudiments	Undivided rudiments or 2–4 cells
4	32–64 cells	Undivided rudiments	2–4 cells
5	64 cells	Undivided rudiments	2–4 cells
6	General liberation		2–4 cells
7	Belated sori	2–4 cells	4 cells
8			4–8 cells
9			8–16 cells
10		Many sori. 64 cells	16 cells
11			16–32 cells
12		General liberation	32–64 cells
13		Belated sori	64 cells
15			General liberation
16			Belated sori

and also the beginning of initiation of rudiments. As a matter of fact, the numerous individuals examined on this day showed considerable differences among themselves. The male plants may be grouped in the following categories: (1) no antheridia empty, new crop not visible; (2) none empty, new crop inconspicuous; (3) very few antheridia empty, new crop conspicuous; (4) antheridia empty near base of plant, not empty near apex, new crop barely visible; (5) antheridia as in no. 4, new crop conspicuous, some of the rudiments 4-celled in surface view; (6) antheridia nearly all empty, new crop

barely visible; (7) antheridia all empty, new crop showing 4 cells. The majority of plants collected on this day were in the fourth or fifth stage.

The tendency toward periodicity in the production of sexual cells is probably a hereditary character. That periodicity is not a series of simple responses to successive stimuli is shown by the observation of WILLIAMS that individuals removed from the influence of the tides continue to show the usual periodicity, and by HOYT's statement that individuals produced by vegetative multiplication

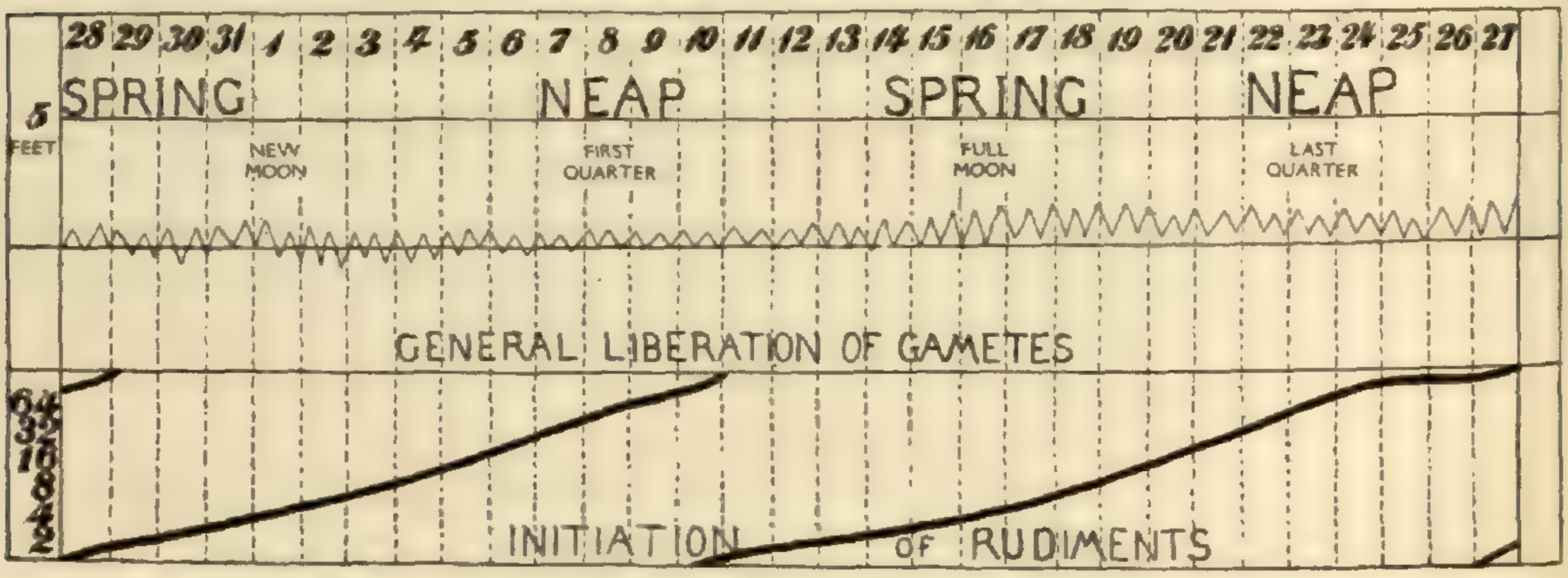

FIG. 1.—Chart showing tidal relations at Naples from March 28 to April 27, 1908, with record of crops of *Dictyota* for the same period. The tide records were furnished by the Italian government, through the kindness of Dr. R. DOHRN, of the Zoological Station at Naples. The chart is to be compared with similar charts for Bangor, Wales, and Beaufort, N.C. (HOYT 2). The zigzag lines show the rise and fall of the tide and the height of the water in relation to the mean low-water mark of spring tides. The curved lines show the development of the sexual crops (male) of *Dictyota* for the respective periods with their relations to the tides. The numbers opposite the crop curves indicate the number of cells seen in the surface view of each antheridium.

and never subjected to the influence of the tides show approximately the same periodicity as those in their natural habitat. The former observation was confirmed by me at Naples, and goes to show that the habit of periodical reproduction is fairly well fixed. The habit, however, must have had its origin in response to external conditions, and it is a matter of considerable interest to ascertain, if possible, what factor or factors gave rise to the periodicity. The only suggestion made thus far is that of WILLIAMS that the effective factor is the increased illumination during low water of spring tides, a view from which HOYT dissents.

WILLIAMS' hypothesis seems inadequate to explain the periodicity at Naples. *Dictyota* flourishes there at a depth of many feet below

the surface, and the difference between the height of low water at spring and neap tides is only 0.25 feet. This slight difference can hardly cause any considerable variation in the total illumination of the plants under consideration, not as much as is caused by alternating cloudy and sunny days. It is interesting to note, however, that both initiation and liberation occur at Naples on the day that low water occurs at or nearest midday. Thus low water at midday occurred at Naples on March 29, April 10, and April 27, 1908, the days when initiation and liberation were found to occur. Whether this is more than a coincidence is still to be seen, but the fact remains that the critical points in the sexual life of *Dictyota* coincide exactly with the periods of maximum intensity of illumination.

If one considers the behavior of *Dictyota* at Naples alone, it seems a fairly satisfactory hypothesis that the effective factor in producing periodicity is the stimulus of the maximum intensity of light. When one comes to apply this hypothesis to the other regions where *Dictyota* has been studied from this standpoint, it becomes evident that, if true at all, the hypothesis is modified by other factors. At Beaufort, for instance, low water at midday occurs two days before new and full moon, while initiation occurs on the day before or the day of the greatest spring tide. At Bangor, on the other hand, low water at midday occurs about five days before new or full moon, and initiation takes place one to two days before the least neaps. At Plymouth low water of the greatest spring tides occurs at midday, and here the times of initiation and liberation coincide more nearly with the periods of neap tides. It is obvious, then, that the simple explanation that might suffice for Naples is not sufficient for other localities, and that the operative factor or factors must be sought by further investigation.

It seems possible that *Dictyota*, in adapting itself to differing conditions at various localities, has acquired its habit of periodicity in response to different factors. That a similar stage in the reproduction of other algae may be induced by different stimuli has been shown by FREUND (1) to be the case in *Oedogonium* and *Haematococcus*. In these forms the external conditions leading to the formation of zoospores differ according to the condition of the individual plants. For instance, cysts of *Haematococcus* form zoospores

(1) when transferred from foul to distilled water, (2) when brought from darkness into light, (3) when water is replaced by sugar solution. KLEBS's investigations (**3**) illustrate the same point for other algae and fungi. Since the fructification of other forms may be induced by different factors, it is possible that the same may be true for *Dictyota* in various situations, and that the factors concerned in inducing periodicity may vary with the locality.

Other organisms, both animals and plants, show a periodicity in the release of sexual cells comparable to that of *Dictyota*. In *Amphitrite ornata*, an annelid worm, "practically all sexual products are deposited within three days of spring tides" (SCOTT **6,** p. 332). KUCKUCK finds (**4**) in *Nemoderma tingitana* that the gametes are released at times of neap tides. TAHARA shows (**7**) that the oospheres of *Sargassum enerve* are released at fortnightly intervals at about the time of new and full moon. Other species of *Sargassum* are said by TAHARA to show a similar periodicity, in which liberation occurs at various intervals after the greatest spring tides.

It is obvious, therefore, that periodicity in the release of sexual cells is a widespread phenomenon, probably to be attributed to various factors in different species, and perhaps to more than one factor in the same species in different localities.

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CURRENT LITERATURE

BOOK REVIEWS

Fungous diseases of plants

Owing to the existence of an extensive system of experiment stations in the United States, one of whose chief activities has been the investigation of plant diseases, the conditions for the accumulation of facts relating to plant pathology have been unusually favorable. Following the progress made in investigation, the teaching of plant pathology has begun to develop chiefly in the agricultural colleges associated with the stations. Thus far, however, there has been no attempt to organize into a comprehensive text the vast material accumulated by plant pathologists and to make it available for teachers, although a need for such work has been felt by those who have attempted to teach the subject. The appearance of DUGGAR'S book[1] on plant diseases is therefore both timely and desirable. The work, as the preface indicates, is designed primarily as a textbook, but its possible service as a reference book has also been kept in view. Aside from the brief historical introduction, it falls into three parts: (1) culture methods and technic, (2) physiological relations, and (3) fungous diseases of plants.

The first part is designed to introduce the student to the methods and manipulations used in the study of fungous diseases. In it are treated the methods of handling apparatus, the preparation of culture media, the cultivation of organisms, and microscopical technic. On the whole, the directions are clear and to the point, and embody many details of manipulation which are acquired only through intimate experience with such work. The use of the freezing method for cutting sections should perhaps have been mentioned, especially as its adaptability for certain kinds of work has been recently emphasized.[2]

The part on physiological relations comprises a discussion of the germination of spores and the modes of life and relation to environmental factors of parasitic fungi, together with chapters on artificial infection, disease control, and the preparation of fungicides. It stands for the whole field which belongs peculiarly to the general subject of plant pathology. Considered from this standpoint, the treatment is surprisingly brief and much that is in the chapter does not belong there. This is especially true of that part of the chapter on germination which deals with methods, part of the section on environmental factors, and nearly all of the chapter on artificial infection. These should have been included in the

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[1] DUGGAR, B. M., Fungous diseases of plants. 8vo. pp. xii + 508. *figs. 240.* Boston: Ginn & Co. (undated).

[2] FREEMAN, E. M., The ether freezing microtome in botanical work. Science N.S. **25**:747–749. 1907.

first part on methods and technic. The field represented by this part has been so greatly enriched in recent times, by the addition of both facts and ideas, that the treatment seems wholly inadequate.

The last part, making up the bulk of the work, deals individually with the plant diseases induced by fungi, under which the author includes the myxomycetes and bacteria. The arrangement is in the order of taxonomic sequence, each chapter representing one of the large divisions of the fungi, as Phycomycetes, Ascomycetes, etc. The individual diseases are treated in numbered sections of the chapters. A section is given to the discussion of each disease, except those of minor importance, which are grouped together. The arrangement serves to bring out the morphological relations of the disease-producing fungi, without laying too much stress on purely morphological and taxonomic features. Some clearness would have been gained if the discussion of orders and families had not been forced into the system under headings coordinate with those under which the individual diseases are discussed. The treatment of the diseases is clear and comprehensive, each being discussed with reference to its distribution, the influence of environmental factors on its occurrence and prevalence, the life history of its causal organism, and the methods of its control. In the relative prominence given to the various diseases, the author has been guided by their economic importance, but the scope has been made broad enough to include all of the common diseases injurious to cultivated crops. A few diseases not occurring in this country have been included, apparently for the sake of completeness. As a rule, the text is conservative and free from innovations at variance with current usage. There is one notable exception, however, in the introduction of a series of newly compounded terms to apply to certain artificial groups of the rusts, based on the number of spore-forms present in the cycle. Thus we have "euautouredo" to include all autoecious rusts possessing all spore-forms, and "opsiautouredo" to include all autoecious rusts lacking the uredo stage, etc. Aside from any criticism that may be offered on account of the faulty composition of these unwieldy terms, the pedagogical soundness of introducing them for the first time through the medium of a textbook may well be questioned.

In matters of detail, the work shows an unusual lack of care in the preparation of the manuscript or in proofreading. The following examples serve as illustrations: on page 54 "Löwitz" is printed for "Löwit"; on page 86 "Scot" for "Scott"; and on page 121, second citation, "Histology" for "History." In the legend of fig. 50 a germinating oospore is described as a "germinating oogonium." On pages 272 and 276 "VON SCHRENK" should read "VON SCHRENK and SPAULDING." On page 337 the citation of MCALPINE should read "Stone-fruit trees" instead of "Stone fruits." *Phoma Betae* is said not to occur in the United States (p. 344), but it has been reported from Colorado and Kansas.[3] On page 386, note, ARTHUR is said to have introduced the terms "*pycnium*, *aecium*,

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[3] ORTON, W. A., Plant diseases in 1907. Yearbook Dept. Agr. 1907:577–589; see also Yearbook 1906:502 (*Phyllosticta Betae* Oud.).

uredinium, and *telium* in substitution for teleuto, uredo, aecidial, and spermagonial stages" of the rusts, instead of the reverse order. On page 467 *Trametes Pini* is said to be the "chief cause of loss among fungi."

On the whole, the book is an excellent presentation of the subject of plant pathology from an American standpoint. Most of its shortcomings relate to individual or minor details. In it the vast amount of material collected through the agencies of the experiment stations and the U.S. Department of Agriculture has been brought together for the first time in an easily available form. The facts presented are largely derived from American work and apply to American conditions. It is sufficiently comprehensive for a textbook, and will be of much service as a reference book in the field which it represents. The style is clear and concise, and the arrangement is that which the teacher would naturally adopt. The free citation of literature is of great service to both student and teacher. The book is abundantly illustrated, and both illustrations and press work are all that could be desired.—H. HASSELBRING.

The morphology of plants

The third and last volume of VELENOVSKÝ'S textbook[4] on the comparative morphology of plants deals with the flower of phanerogams, the ovule, pollination, embryo, seed, fruit, and the evolution of plants. Fertilization, parthenogenesis, and polyembryony are treated under the section on the ovule, preceding the description of pollination. The volume opens with the following definition of a flower: "The flower of phanerogams is a shortened axis of limited growth, which carries foliar organs adapted to the purposes of fertilization." We are assured that this definition applies to all cases except the female structures of the genus *Cycas*, which are not regarded as flowers.

The book deals almost entirely with the grosser external features of plants, little attention being given to the details of development. It must be confessed that the phase of morphology represented by this book is somewhat neglected by modern morphologists, who are likely to pay insufficient attention to the taxonomic side of botany. Morphologists should find the work useful as a reference and as a supplement to their taxonomy; but as a complete textbook of morphology it is not comprehensive enough to meet modern demands.—CHARLES J. CHAMBERLAIN.

NOTES FOR STUDENTS

The cretaceous plants of Japan.[5]—This interesting product of the Anglo-Japanese understanding represents the structural study of partly calcified and partly silicified nodules from the Upper Cretaceous of Hokkaido in northern

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[4] VELENOVSKÝ, JOS., Vergleichende Morphologie der Pflanzen. Vol. III. pp. 478. *pls. 6–9. figs. 400.* Prag: Fr. Řivnáč. 1910. For review of vols. I and II see BOT. GAZETTE **44**:310. 1907.

[5] STOPES, MARIE C., and FUJII, K., Studies on the structure and affinities of cretaceous plants. Phil. Trans. Roy. Soc. London B **201**:1–90. *pls. 1–9.* 1910.

Japan. Only in rare instances were the authors able to make out the external form of the material studied, and in no case do they seem to have been able to correlate it with the extremely abundant cretaceous genera known from impressions. To this initial disadvantage is added a not entirely satisfactory familiarity with the anatomical structure of living angiosperms and conifers. The eighteen species described as new in the memoir are consequently in some cases not really new, since they represent the parts of plants already known from impressions and recently identified structurally by American paleobotanists. In other instances the anatomical characterization is too vague and indefinite for subsequent use. In spite of these drawbacks, the memoir under discussion must rank as one of the most important recent contributions on the cretaceous flora, and it is much to be desired that the authors may be able to continue their investigations as they promise to do.

Of the eighteen species described, four are cryptogamic, one being a fungus and three others ferns. An interesting cycad-like leaf, *Niponophyllum*, is described which differs from the leaf structure of living cycads in the complete absence of centrifugal wood, all the xylem being of the cryptogamic centripetal type.

Of the other gymnosperms described, the most interesting is *Yezonia*, which is considered by the authors to represent a new genus, and of which they state "it is impossible to find any family among the gymnosperms with which we can satisfactorily include this plant." This view of the matter will hardly stand, since in every detail of structure it corresponds absolutely with *Brachyphyllum*, the commonest conifer of the later Mesozoic, which, moreover, on anatomical grounds has been recognized recently as an araucarian conifer. Another gymnospermous branch is also described under the new generic name *Cryptomeriopsis*. Of this it may be stated that the description given of its internal organization by the Anglo-Japanese authors parallels with fidelity, so far as it goes, that of *Geinitzia Reichenbachi*, recently described structurally from the North American Cretaceous. Two imperfect coniferous cones are likewise characterized, *Yezostrobus* and *Cunninghamiostrobus*. One *Araucarioxylon* and two species of *Cedroxylon* complete the list of coniferous remains.

Either as the result of a bad condition of preservation, or a failure to realize clearly the importance of detailed description, four angiospermous ligneous genera, all considered to be new (*Jugloxylon*, *Populocaulis*, *Fagoxylon*, *Sabiocaulis*), are insufficiently characterized. The detailed structure of the rays, the characters of the vessels and wood fibers, as well as the distribution of wood parenchyma, all important features in the description of angiospermous fossil woods, are entirely or almost entirely omitted. If the omission is due to faulty preservation, the woods are scarcely worth publishing. The genus *Sauropsis* is somewhat more clearly characterized. One genus (*Cretovarium*) representing a tricarpellary ovary is likewise described, but as the accompanying vegetative organs and even any considerable part of the floral apparatus itself are absent, it seems impossible to arrive at any satisfactory conclusion as to its affinities. One curious and unfortunate omission throughout the memoir is the almost com-

plete failure to indicate the magnification used in the figures. This makes comparisons on the part of other workers difficult or even impossible.

In spite of the exceptions taken in various respects to the work of the Anglo-Japanese authors, it must be conceded that their line of investigation is one of great promise, and it is to be hoped that they will feel encouraged to continue it with a greater attention to definiteness in anatomical characterization.—E. C. JEFFREY.

Vascular anatomy of Gleichenia.—BOODLE and HILEY,[6] from the study of the anatomy of *Gleichenia pectinata* and allied species, reach certain theoretical conclusions as to the origin of the tubular medullated stele. They report the result of the examination of the node and internode, as well as the branching stem, of certain species of *Gleichenia*, particularly *G. pectinata*. It is not surprising that they reach substantially the conclusions which have been published already by the senior author in earlier contributions. The published results in this case, however, appear to indicate a certain modification of the position originally held by BOODLE, to the effect that in all cases the pith is a part of the stele and is not derived by inclusion of the fundamental or ground tissue from outside the central cylinder; for the authors in this article use the term solenostelic, borrowed from GWYNNE-VAUGHAN and employed by him in the sense of a tubular stele with internal as well as external phloem and inclosing fundamental tissue as a pith (a meaning stated by GWYNNE-VAUGHAN himself to be equivalent to the reviewer's siphonostelic with internal phloem). Although the English writers in this instance concede apparently the arrival of the solenostelic condition as the final result of the modification of the pithless protostele, they express the opinion that the pith appears first as the result of the transformation of some of the tracheids into a central mass of parenchyma, a condition followed by the appearance of ramular gaps in the stele as the result of branching, leading to the intrusion of phloem from the outside of the stele and ultimately of the fundamental tissue itself. Only at the end of the process do the leaf gaps appear and become patent.

These views are all the more remarkable because in the same article the authors concede that the islands of parenchyma occurring in the petiolar strands of certain representatives of the Gleicheniaceae are derived from the cortex by inclusion, and were originally surrounded both by internal phloem and internal endodermis. The condition in which the included parenchyma is separated from the vascular tissues of the petiole by neither endodermis nor internal phloem is a result of progressive degeneracy. It appears almost an extreme example of the perversity of the human mind to explain the occurrence of central parenchyma in the leaf trace in a node diametrically opposite to that adopted for the appearance of a pith in the vascular tissues of the stem. If the fundamental tissues may be included in the leaf trace, there appears to be no reason why a similar process should not lead to the formation of pith in the axis. The adoption of this hypoth-

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[6] BOODLE and HILEY, On the vascular structure of some species of *Gleichenia*. Annals of Botany **23**:419–432. *pl. 29*. 1909.

esis, moreover, explains the appearance of included endodermis and phloem in young individuals of various examples of vascular plants, a condition which finds no elucidation whatever in connection with the views adopted almost universally by English anatomists.—E. C. JEFFREY.

Jurassic woods.—GOTHAN[7] describes a number of fossil woods from the Jurassic of King Karl's Land, none of which he refers to the Araucarineae. Two species, *Phyllocladoxylon* sp. and *Xenoxylon phyllocladoides*, are considered to belong in the region of the Podocarpineae. One *Cupressinoxylon* is also figured, which is compared with the *C. McGeei* of KNOWLTON. Next are two Cedroxyla, *C. cedroides* and *C. transiens*. To the latter of these he attaches much importance because of the presence of araucarian pitting together with the ray structure of the Abietineae. The author assumes that he has to do in this instance with an abietineous wood, in which certain araucarineous characters indicate the derivation of the Abietineae from an araucarian stock, in accordance with the conventional and generally received views. It does not seem to have occurred to the author that he may have an araucarian conifer with indications of transition toward the Abietineae. The genus *Araucariopitys*, recently described by the reviewer, has the same ligneous characters as GOTHAN'S *Cedroxylon transiens*, only with a more pronounced resemblance to the Abietineae. It is nevertheless unquestionably an araucarian conifer. One abietineous wood is described, namely *Protopiceoxylon extinctum*. The wood in question has normally only horizontal resin canals, but vertical ones may occur as the result of injury. The author regards his wood as evidence that the vertical type of resin canal is older than the horizontal, forgetful that GOEPPERT and PENHALLOW have described much older Pityoxyla from the Carboniferous and Permian respectively, which show only horizontal canals. It seems, accordingly, that "*Protopiceoxylon*," with a much greater degree of probability, represents a stage in degeneracy toward the *Cedroxylon* type, rather than a primitive abietineous type antedating *Pityoxylon*. The author lightly sets aside the evidence adduced on comparative anatomical and experimental grounds by the reviewer for the great age of the pinelike Abietineae. With admirable Teutonic frankness, he characterizes the reduction hypothesis of the phylogeny of the Coniferales as one to which, "wohl niemand beipflichten kann." He apparently loses sight of the fact that the reduction hypothesis is now quite generally adopted by competent morphologists for such degenerate groups as the Equisetales, Lycopodiales, etc. Had the literature on the fossil conifers, which has recently been published by American paleobotanical writers, been available, in all probability GOTHAN'S opinion in regard to the fallacy of the reduction hypothesis in connection with the phylogenetic development of the conifers would have been expressed with considerably more reserve.—E. C. JEFFREY.

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[7] GOTHAN, W., Die Fossilen Hoelzer Koenig Karls Land. Handl. Kgl. Svensk. Vetensk.-Akad. **42**: no. 10.

Chemotropism of roots.—In a preliminary paper, PORODKO[8] reports upon the chemotropism of the roots of *Lupinus albus* and *Helianthus annuus*. Roots 20–35 mm. long were placed in a lamella of agar varying in thickness from 6 to 60 mm., which separated the solution used from water. In all, 50 chemical substances were used, the concentration of which varied from 0.1 *n* to 0.001 *n*. As a rule, the roots did not remain straight, but bent against or with the diffusion stream. The range of concentration between maximum and minimum depended upon the substance used and the thickness of the agar lamella. Concentrations close to the maximum caused bending against the diffusion stream or positive response, which effect was observed with both electrolytes and non-electrolytes. PORODKO considers this a traumatropic response, due to the inhibition of growth on the up-stream side of the root. With lower concentrations, electrolytes and non-electrolytes affect the roots differently. The former cause great regularity as regards the direction of bending of the root, while the latter produce positive, negative, and intermediate responses. Acids, alkalies, and carbonates cause positive, and neutral salts negative bendings. The responses due to H and OH ions are considered to be traumatropic. The amount of negative response seems to depend upon the cation, being greater in the presence of one with a double charge than in the presence of one with a single charge. In many cases the responses are not all of one kind. Nevertheless, it is necessary to explain the cause of all. From his experiments, PORODKO concludes that positive but not negative responses can take place in decapitated roots, and that the latter, but not the former, show up as after-effects, although only on the clinostat. The two reactions are different in nature, the positive being passive and caused by the inhibitory effect of the greater concentration on the growing region on the up-stream side of the root, the negative being active and due to the chemotropic effect of the diffusion stream, which tends to accelerate the growth on the up-stream side. Hence, upon the growing region of a root of *Lupinus albus* subjected to the influence of the diffusion stream of a chemical substance, two antagonistic tendencies are at work, the direction of bending of the root being dependent upon the relative strengths of the two tendencies. Roots of *Helianthus annuus* act differently from those of *Lupinus albus*, in that they show only traumatropic response, but why this is true is not known.—R. CATLIN ROSE.

National Academy of Sciences.—At the annual session of 1910 two botanical papers were presented (April 19), which may be outlined as follows:

"The distribution of *Agave* in the West Indies," by WILLIAM TRELEASE.—Three main types of *Agave* are recognized in the West Indies: one confined to the southwestern Cuban region, another to the Inaguas, and the third ranging through the entire archipelago. Subtypes of the latter are limited respectively to the Greater Antilles, the Bahamas, the Caribbees and the Leeward Islands, and the

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[8] PORODKO, THEODOR, Ueber den Chemotropismus der Wurzel. Ber. Deutsch. Bot. Gesell. **28**:50–57. 1910.

adjoining Venezuelan coast. Within these groups specific differentiation is observable, so that each island isolated by a 100-fathom channel has its endemic species, the islands with a common coastal plain possessing little if at all differentiated forms. The almost entire absence of the genus from South America and the geographic grouping of species and superspecies in the West Indies indicate that *Agave* penetrated from the Central American mainland, where it centers, and overran the terrain before the disruption into islands, two or perhaps three parent stocks being involved.

"The vascular plate and cotyledons of gymnosperms," by JOHN M. COULTER. —Among the various vascular structures of gymnosperms that have been used to suggest progressive evolutionary changes, the vascular plate of the cotyledonary node is perhaps as significant as any, especially its connections with the cotyledons. Series of cycads, of conifers, and of other gymnosperms were shown to illustrate the following general tendencies: to reduce the cotyledons to two, to reduce the protoxylem poles of the vascular plate (and hence the root poles) to two, to eliminate certain vascular connections of the cotyledons, and to restrict the branching of strands within the cotyledons.

Differentiation among chromosomes.—*Crepis virens* seems to afford promising material for the solution of several difficult cytological problems. JUEL had already found the diploid and haploid numbers in *C. tectorum* to be 8 and 4. ROSENBERG[9] now finds the numbers in *C. virens* to be 6 and 3, the lowest numbers yet established for plants. The fact that the chromosomes are so few and that they are readily recognized as "prochromosomes" in the resting nucleus, removes any danger of uncertainty in counting which might be anticipated in case of large numbers. Not only is the number low, but the individual chromosomes are not alike, two being long, two rather short, and two intermediate. In the diploid divisions these three kinds of chromosomes appear in pairs, the members of a given pair being alike. At synapsis a double thread appears, and there is a fusion which is to be regarded as a fusion of whole chromosomes, reduction in number being brought about in this way. ROSENBERG suggests that interesting results might be obtained by crossing *Crepis virens* and *C. tectorum*, and he promises to make the attempt.

Noting the low number of chromosomes in *Crepis tectorum* (8 and 4) and in *C. virens* (6 and 3), TAHARA[10] examined the Japanese species, *C. japonica*, and found the numbers to be 16 and 8, just double the numbers in *C. tectorum*. The chromosomes were also found to be of different sizes and forms. If there is a relation between specific characters and chromosomes, the genus *Crepis* would seem to the reviewer to be a favorable form for the investigation of this subject.—CHARLES J. CHAMBERLAIN.

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9 ROSENBERG, O., Zur Kenntniss von den Tetradenteilung der Compositen. Svensk. Bot. Tidskrift **3**:64–77. *pl. 1.* 1909.

10 TAHARA, M., Ueber die Zahl der Chromosomen von *Crepis japonica* Benth. Bot. Mag. **24**:23–28. *pl. 2.* 1910.

Interaction between scion and stock.—MEYER and SCHMIDT[11] have produced a voluminous article on the interchange of substances and mutual influence between stock and scion in a heteroplastic graft. The introduction and review of literature occupy 48 pages, and 33 pages are given to the statement of results and the summary. One is compelled to think that the article could have been advantageously condensed to half the space. The authors mention that interchange of carbohydrates was already fully worked out, while the previous work on movement of aplastic and other substances is very unsatisfactory. They direct their attention to the movement, formation, and storage of alkaloids, using *Nicotiana Tabacum* as scion on *N. affinis* and *Solanum tuberosum* as stocks, and *Datura Stramonium* as scion on *Solanum Lycopersicum* and *S. tuberosum*. They find that alkaloids can pass from scion to stock; but the movement is very slow, and apparently takes place through the parenchyma and not through the sieve tubes. With *N. Tabacum*, normally rich in nicotin, as scion, and *N. affinis*, normally poor in nicotin, as stock, the latter comes to contain many times its normal amount of nicotin, and even ten times as much as the scion; while the scion becomes relatively poor in it. With *S. tuberosum* as stock for *N. Tabacum*, the periderm cells of the former become the main storage tissue for the nicotin. It is most abundant in the tissue of the stock just below the graft, and decreases in amount as the cells are more distant; while in the tuber none at all or only traces appear.—WILLIAM CROCKER.

Living cells and extreme temperatures.—GEORGEVITCH,[12] in investigating the effect of extreme temperatures on living cells, used the root tips of *Galtonia candicans*. They were kept at 40° C., and −5° C., killed and fixed at the same temperature, and the effect of these extremes noted. At a temperature of +40° C., the cytoplasm coagulates and forms small clumps of dark-staining material. At low temperatures the cytoplasm becomes vacuolate, and the coordination in the action of the spindle fibers is broken up, which results in the distribution of chromosomes between the poles. The activity of the kinoplasm is decreased by low temperature and increased by high temperature. There result larger spindles with stronger fibers, more rapid transport of chromosomes, and shortened duration of nuclear division. Thereby cell wall formation is inhibited and binucleate cells are of frequent occurrence. The chromosomes often form chains, due to the irregular transport toward the poles. In cold preparations the nucleus often takes on an amoeboid form, also in the warm, but not to such an extent. In general it can be said that high temperatures favor development of chromatic

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[11] MEYER, ARTHUR, and SCHMIDT, ERNST, Ueber die gegenseitige Beeinflussung der Symbionten heteroplastischer Transplantationen mit besonderer Berücksichtigung der Wanderung der Alkaloide durch die Pfropfstellen. Flora **100**:317–396. *figs.* 3. 1910.

[12] GEORGEVITCH, PETER, Ueber den Einfluss von extremen Temperaturen auf die Zellen der Wurzelspitze von *Galtonia candicans*. Beih. Bot. Centralbl. **25**:127–135. 1910.

material, while low temperatures inhibit it. In cold preparations one finds collections of chromatin which stain blue and are called pseudonucleoli. SCHRAUMEN found the same in the cells of shoots of *Vicia Faba* kept at both high and low temperatures. GEORGEVITCH did not find them in warm preparations. In cold preparations the nucleoli show an increase in size, mass, and numbers.—R. CATLIN ROSE.

Fossil Osmundaceae.—KIDSTON and GWYNNE-VAUGHAN[13] have continued their interesting investigations on the fossil Osmundaceae. In the case of the most important of the species which they describe (*Thamnopteris Schlechtendalii* Eichwald) there can apparently be no doubt that they have really to do with the remains of an osmundaceous fern. They find that in this species the center of the stele is marked by the presence of a mass of short tracheids without any admixture of parenchyma, which curiously enough they regard as the equivalent of a pith. It is surely begging the question as to the origin of medullary structures, to regard tissues which admittedly are entirely tracheary and contain not the slightest admixture of parenchymatous cells as equivalent to the medulla of the higher plants. The difficulty of regarding the central mass of short tracheids in *Thamnopteris* as a pith is rendered insuperable, apparently, by the fact that the leaf traces originate from the stele exactly as in those cases where no pith is present, that is without giving rise to any foliar gaps. The views entertained by the present authors and the majority of English writers on anatomy encounter an additional difficulty in that they are quite unable on their hypothesis to explain the presence of internal phloem and internal endodermis in closed steles. These find apparently a very simple and natural elucidation in connection with the reduction theory now advocated by a considerable number of American anatomists.—E. C. JEFFREY.

Bennettitales.—NATHORST[14] has described the more or less complete reproductive apparatus of a number of bennettitean forms. There are three species of *Williamsonia* from the Jurassic beds of Whitby and Scarborough, England. In these were found in different cases both microsporangia with microspores, and seeds. The structure of the microspores is illustrated by admirable photomicrographs. A new genus (*Wielandiella*) has a very remarkable vegetative organization. The stem branches freely in an apparently dichotomous manner and is quite slender. The cones occur in the forkings of the branches. The vegetative structure resembles that of the problematic *Anomozamites*. The cones showed remains of both pollen and seeds. The structure of the microspores of a third genus (*Cycadocephalus Sewardi*) is described. These are remarkable for their close resemblance to fern spores. For comparison, a figure of *Wel-*

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[13] KIDSTON, R., and GWYNNE-VAUGHAN, D. T., On the fossil Osmundaceae. III. Trans. Roy. Soc. Edinburgh **46**:1909.

[14] NATHORST, A. G., Paleobotanische Mitteilungen. 8. Handl. Kgl. Svensk. Vetensk.-Akad. **45**: no. 4. 1910.

trichia Fr. Braun from the Mesozoic of Franconia is introduced. The result of the present important communication is to enlarge our knowledge of the male organs of the Bennettitales by seven different species belonging to five different types. Two species of *Williamsonia* have monosporangiate strobili. The same condition is clearly demonstrated in *Cycadocephalus*. The author wisely refuses to commit himself as to the nature of the Bennettitean inflorescence, and avoids any reference to its possible homology with the angiospermous flower. —E. C. JEFFREY.

Rôle of ammonium salts.—PRIANISCHNIKOW,[15] working with grasses, has already shown that a substitution in sand cultures of $\frac{1}{4}$–$\frac{3}{4}$ of the $NaNO_3$ by $(NH_4)_2SO_4$ increases the power of the plant to gain phosphoric acid from raw phosphates (phosphorite), while in absence of $(NH_4)_2SO_4$ the plants show phosphoric acid starvation. Total substitution, however, greatly reduces the harvest. Both these effects are attributed to the released sulfuric acid. In partial substitution the acid was strong enough to aid in dissolving the phosphorite, and in total substitution so strong that it greatly injured the plants. It is also shown that $CaCO_3$ is very effective in preventing injuries by $(NH_4)_2SO_4$, and if only $\frac{1}{4}$–$\frac{1}{2}$ enough was used to neutralize the liberated sulfuric acid, the consumption of the phosphorite was also much favored. In working with barley, peas, and buckwheat, the author has determined that mixtures of $NaNO_3$ and $(NH_4)_2SO_4$ are better sources of nitrogen than either one alone, for, as he states, the first is physiologically basic (base liberated due to the consumption of NO_3 as source of nitrogen) and the second physiologically acid (acid liberated due to the consumption of NH_4 as the source of nitrogen). The two maintain the culture medium neutral. The author does not attempt to decide between the relative values of ammonium salts and nitrates as a source of nitrogen when the former are of very weak acids, as those used by RITTER[16] to settle this question for fungi.—WILLIAM CROCKER.

Fossil conifers.—NATHORST[17] has described with truly admirable clearness and judgment the cones of the problematical coniferous genus *Palissya* from the Rhaetic of Schonen in Sweden. The ovuliferous cone scales are characterized by the presence of two rows of opposite seeds, with very loose integuments or epimatia. The author concludes that the evidence of the organization of the cone scales tends to connect the genus with a second genus described in the article, namely *Stachytaxus*. This genus has yewlike foliage, and attached to the ends of the twigs are lax cones with distant scales, each of which bears two ovules, provided with a widely flaring integument or possibly an epimatium comparable with that found in the Taxineae. The author argues for the taxineous affinities

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[15] PRIANISCHNIKOW, D., Zur physiologischen Characteristik der Ammoniumsalze. Ber. Deutsch. Bot. Gesell. **26**[a]:716–724. 1909.

[16] Ber. Deutsch. Bot. Gesell. **27**:582–588. 1909.

[17] NATHORST, A. G., Paleobotanische Mitteilungen. 7. Handl. Kgl. Svensk. Vetensk.-Akad. **43**: no. 8. 1909.

of *Stachytaxus*, and by implication for the similar relationship of *Palissya*. The only real evidence for the affinity of these two genera with the Taxineae seems to rest on the possible presence of an epimatium in connection with the seeds. It seems not improbable that they are really representatives of an araucarian stock different from any now in existence. Some of the later mesozoic Araucarineae possess both the biovulate cone scale and the flaring integument of the genera under discussion. Present indications are that all the mesozoic conifers will ultimately be arranged either under the Abietineae or the Araucarineae in the broader sense.—E. C. JEFFREY.

Orchid flowers and formative stimuli.—FITTING'S work on the effect of pollination and other stimuli upon the postfloration behavior of orchid flowers has been reviewed in this journal.[18] In a second paper,[19] he gives an account of further experimentation of the same kind, and concludes that the changes induced in the perianth, gynostemium, and ovary are at most six, namely: (1) shortening of the life of the perianth, (2) lengthening of the life of the perianth, (3) closing of the flower, (4) swelling of the ovary and gynostemium, (5) fading of the perianth, (6) greening of the ovary and perianth. Each of these may result separately or with several others, in various combinations. Although it seems probable that the influence of the pollen is due to a chemical substance soluble in water and alcohol, FITTING was unable to isolate it in pure form or to identify it. It was determined, by extracting pollen of *Cattleya Trianaei* with water and hot alcohol, that this chemical substance is not found inside the pollen grain, but merely adheres to it and can be removed without injury to the pollen. By using the pollen from which this substance has been removed, the effects of the pollen tube alone can be studied, when it is found that the tube produces the same results as the active substance. This is not due to the substance secreted by the tube or carried down from the pollen grain, but to an unknown factor.—R. CATLIN ROSE.

A new case of apogamy.—*Burmannia coelestis*, as described by ERNST,[20] furnishes a case of apogamy somewhat different from any hitherto reported. From the cells of the egg apparatus of an eight-nucleate embryo sac with diploid nuclei, one and often two and sometimes three embryos are produced. The formation of a tetrad of megaspores is either irregular or completely suppressed, as is already known to be the case in most apogamous forms previously described. No synapsis stage or heterotypic mitosis was observed. The number of chromosomes was not determined, but is greater than in normally fertilized species of *Burmannia*. The anticipated irregularities in the pollen were found, and the

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[18] BOT. GAZETTE **47**:479. 1909.

[19] FITTING, H., Weitere entwickelungsphysiologische Untersuchungen an Orchideenblüten. Zeitschr. Bot. **2**:225–267. 1910.

[20] ERNST, A., Apogamie bei *Burmannia coelestis* Don. Ber. Deutsch. Bot Gesell. **27**:157–168. *pl. 7*. 1909.

fact that fertilization is very easily demonstrated in normally fertilized species makes the writer confident that the failure to find it in *B. coelestis* is evidence that it does not occur. The figures show only topography, without any details of the chromatin situation. A careful counting of chromosomes at critical stages, and a few figures at the stages which show whether a form is apogamous or not, would have extended the paper but little, and would have made unnecessary any further work upon the subject; but as it is, a forthcoming paper will deal with these details, the present one being preliminary.—CHARLES J. CHAMBERLAIN.

Spermatogenesis in Mnium.—As a result of their studies of several species of mosses, the Drs. VAN LEEUWEN-REIJNVAAN reported that in the last division of the spermatogenous cells a second numerical reduction of chromosomes takes place. In a species of *Mnium* having eight chromosomes in the last division, two long and two short chromosomes pass to the daughter cells. WILSON,[21] studying *Mnium hornum*, in a preliminary note announces that no such reduction is found, and that the gametophyte number is constant throughout spermatogenesis. The resting nucleus before the final division is quite large and contains a small nucleolus. A continuous spirem is not present, and the chromatic material appears as a number of small masses from which the chromosomes are formed. In the final division the axis coincides with the long axis of the cell, there being no diagonal division. Six chromosomes can easily be distinguished in the last division, and it is clear that no such reduction as described by the Drs. VAN LEEUWEN-REIJNVAAN takes place in *Mnium hornum*.

It is to be hoped that the final paper will also deal with fertilization, for many investigators find some difficulty in accepting the account given by the Drs. VAN LEEUWEN-REIJNVAAN.—W. J. G. LAND.

Hydrogen bacteria.—The epoch-making researches of WINOGRADSKI (1887–) on the sulfur, nitrite, and nitrate bacteria established the important fact of the existence of non-chlorophyll organisms that are obliged to manufacture their organic food by energy obtained from the oxidation of various simple inorganic substances. In 1906 various investigators reported the existence of bacteria that can oxidize hydrogen as the source of energy for assimilating CO_2. The forms were shown to be capable of using organic food as well, and are therefore facultatively autotrophic, in contrast to the obligate autotrophic forms studied by WINOGRADSKI. LEBEDEFF[22] now makes a preliminary report of the main results of an extensive study of the metabolism of these forms. The fixing of 100 c.c. of CO_2 requires the oxidation of 500–1500 c.c. of H_2. The oxygen for the process is best obtained from atmospheric oxygen, but in absence of it nitrates can be decomposed as its source. The oxidation of H_2 still continues in the presence of organic food, but no CO_2 is fixed in that case.—WILLIAM CROCKER.

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[21] WILSON, M., Preliminary note on the spermatogenesis of *Mnium hornum*. Annals of Botany **24**:235. 1910.

[22] LEBEDEFF, A. J., Ueber die Assimilation des Kohlenstoffes bei Wasserstoff oxydierenden Bakterien. Ber. Deutsch. Bot. Gesell. **27**:598–602. 1910.

Proteases.—VINES,[23] in continuing his work on the proteolytic enzymes of plants, finds that both malt extract and taka-diastase (Parke Davis and Co.) contain enzymes capable of digesting fibrin and of splitting peptone. From malt extract he has isolated the peptone-splitting enzyme free from the fibrin-digesting body, and from taka-diastase he separated each from the other. Both these enzymes seem to act best in acid media. In animal tissues there are two fibrin-splitting enzymes: α protease, weak and acting in basic media; and β protease, more powerful and acting in acid media. By special methods of preparation, VINES obtained a protease which acted best in neutral and basic media. This perhaps corresponds to the α protease of animal tissues. The ereptases, peptone-splitting enzymes, of animal tissues act best in basic media. VINES'S work shows that plant ereptases act in acid media. As to terminology, one is inclined to believe that VINES could adopt profitably that of animal workers as given by VERNON.[24]—WILLIAM CROCKER.

A new genus of Cordaitales.—SCOTT and MASLEN[25] have described a new genus (*Mesoxylon*) of Cordaitales from the calcareous nodules of the Lower Coal-measures of Lancashire. It is intermediate between *Poroxylon* and *Cordaites*, as its name implies, including five species which have been referred heretofore to these two genera. The combination of characters is the anatomical habit of *Cordaites* and the centripetal xylem of *Poroxylon*. The pith is relatively large and discoid (as in *Cordaites*); the wood is dense, with narrow pith rays and relatively small tracheids; the leaf traces are double, but divide before entering the leaf; the centripetal xylem is present in the leaf traces at the margin of the pith (as in *Poroxylon*) and throughout their course to the leaves. The genus is thought "to completely bridge the gap, so far as anatomy is concerned, between the Poroxyleae and the Cordaiteae," and helps to connect the cordaitean and later forms (excepting cycadophytes) with the "pteridosperms."—J. M. C.

"Bars of Sanio" in Coniferales.—The "bars of Sanio" are "folds" of cellulose to be observed in the walls of tracheids as horizontal or more or less semicircular markings, which stand out clearly with proper staining. Miss GERRY[26] has investigated their distribution among the Coniferales, and has discovered that they furnish a constant and useful character in the determination of fossil woods. They were found in 35 of the living genera, but do not occur in *Agathis* and *Araucaria*, nor in the mesozoic araucarians. Since they do occur in the podocarps, it is concluded that this group is more closely related to the Abietineae than to the Araucarineae, a conclusion which contradicts a growing conviction based

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[23] VINES, S. H., Proteases of plants. Annals of Botany **24**:213–222. 1910.

[24] VERNON, H. M., Intracellular enzymes. London: John Murray. 1908.

[25] SCOTT, D. H., and MASLEN, A. J., On *Mesoxylon*, a new genus of Cordaitales (preliminary note). Annals of Botany **24**:236–239. 1910.

[26] GERRY, ELOISE, The distribution of the "bars of Sanio" in the Coniferales. Annals of Botany **24**:119–124. *pl. 13*. 1910.

on other characters. It is an interesting fact that the ancient *Prepinus* shows these "bars," which fact helps to establish their ancient character. The total result is to emphasize strongly the distinctness of the araucarians from all the other Coniferales.—J. M. C.

Embryo sacs of some Onagraceae.—An investigation[27] of *Epilobium angustifolium*, *E. Dodonaei*, *Oenothera biennis*, and *Circaea lutetiana* shows an interesting variation from the conventional development of the embryo sac. The usual tetrad of four megaspores is formed and the lowest one enlarges and begins to develop in the well-known way, but as soon as the four-nucleate stage is reached, two synergids and an egg are formed at the micropylar end of the sac, leaving one free nucleus in the middle or toward the antipodal end. This sac looks like that of *Cypripedium*, as described by Miss PACE,[28] but is formed from one megaspore, while that of *Cypripedium* is formed from two. At fertilization, one male nucleus fuses with the nucleus of the egg and the other with the single polar nucleus, so that there is no triple fusion as in *Cypripedium*, where one of the synergids takes part. The embryo and endosperm develop in the usual way.—CHARLES J. CHAMBERLAIN.

The original Oenothera Lamarckiana.—GATES[29] has discovered a manuscript in the Sturtevant collection of the library of the Missouri Botanical Garden "which proves that this plant was originally a species growing wild in Virginia, and that it was the first *Oenothera* introduced into European gardens, about 1614." In view of the fact that the origin of this important species has been in doubt, and that it has been claimed to have originated in cultivation, this discovery is noteworthy. The record referred to is in the form of a long marginal note in a copy of BAUHIN'S *Pinax*, by JOANNIS SNIPPENDALE, and is an accurate description of the plant. "The record is as complete and accurate as could be desired, to prove to one familiar with the characters of these forms the identity of the plants in question." The plant was described under BAUHIN'S name, *Lysimachia lutea corniculata*.—J. M. C.

Color inheritance in Lychnis.—SHULL[30] has discovered that the purple color in *L. dioica* is a compound character, produced by the interaction of three distinct and independent genes. The two types of purple color present in different individuals are a reddish purple, changed to blue by alkalies, and a bluish purple, changed to red by weak acids. The bluish or alkaline color is hypostatic to the reddish or acid color, which is the reverse of the condition found in all other

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[27] MODILEWSKI, J., Zur Embryobildung von einigen Onagraceen. Ber. Deutsch. Bot. Gesell. **27**:287–292. *pl. 13*. 1909.

[28] BOT. GAZETTE **44**:353–374. *pls. 24–27*. 1907.

[29] GATES, R. R., The earliest description of *Oenothera Lamarckiana*. Science N.S. **31**:425, 426. 1910.

[30] SHULL, GEORGE H., Color inheritance in *Lychnis dioica* L. Amer. Nat. **44**:83–91. 1910.

plants containing similar series of colors. It is inferred that crosses between white-flowered plants should result not infrequently in progenies of all purple-flowered offspring, or of purple and white in the ratios 1:1, 3:5, or 1:3; but as yet these results have not been found.—J. M. C.

Jurassic flora of Normandy.—LIGNIER[31] has added a number of new species to the rich jurassic flora of Normandy, that are suggestive of relationships concerning which real knowledge is very much desired. The Filicales are represented by species of *Lomatopteris* and *Linopteris*, and the Equisetales by a species of *Equisetites*. The cycadean forms, however, are of chief interest and abundance, and it would be a great gain to know definitely what the numerous species of *Zamites* and *Otozamites* represent. The conifers are represented by species of *Brachyphyllum*, *Pachyphyllum*, and *Conites*.

The memoir is undated, but its reception in March 1910 suggests recent publication.—J. M. C.

Apospory and apogamy in Trichomanes.—GEORGEVITCH[32] has investigated *Trichomanes Kaulfussii*, whose apospory and gemma production was described by BOWER in 1894. The branching filamentous prothallium bears sterigmata (singly or in tufts), at the ends of each of which is balanced a gemma. The development of prothallia from these gemmae is described in detail, and antheridia were observed developing directly upon the gemmae, sometimes associated with a prothallium on the same gemma. This transition from sporophyte to gametophyte is accompanied by no reduction in the number of chromosomes. Counts were made in both generations and at different stages of mitosis, and always approximated 80.—J. M. C.

Parasitic fungi of Wisconsin.—In 1884 TRELEASE published a list of the parasitic fungi of Wisconsin, and supplementary lists were issued by DAVIS in 1893, 1897, and 1903. Now a fourth supplementary list has appeared.[33] It contains a list of 76 forms occurring on hosts not previously recorded; and 113 forms not reported heretofore from the state. The latter list includes 9 new species and varieties in the following genera: *Ascochyta*, *Cercospora*, *Cylindrosporium* (2), *Gloeosporium*, *Phyllosticta* (2), *Ramularia*, and *Septoria*. This record in reference to 189 forms indicates what interest and persistence can do for any area.—J. M. C.

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[31] LIGNIER, OCTAVE, Végétaux fossiles de Normandie. VI. Flore jurassique de Mamers (Sarthe). Mém. Soc. Linn. Normandie **24**: pp. 48. *pls. 2. figs. 7.* (Undated.)

[32] GEORGEVITCH, PETER, Preliminary note on apospory and apogamy in *Trichomanes Kaulfussii* Hk. et Grew. Annals of Botany **24**:233, 234. *figs. 7.* 1910.

[33] DAVIS. J. J., Fourth supplementary list of parasitic fungi of Wisconsin. Trans. Wis. Acad. Sci. **16**:739–772. 1909.

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BOTANICAL GAZETTE

AUGUST 1910

THE MORPHOLOGY OF THE PODOCARPINEAE

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 138

MARY S. YOUNG

(WITH PLATES IV–VI)

Previous to 1902 the morphology of the Podocarpineae was an unknown field, but recently, through the contributions of COKER (**5**), JEFFREY and CHRYSLER (**7**), BURLINGAME (**2**), BROOKS and STILES (**1**), and YOUNG (**25**) on *Podocarpus* and *Dacrydium*, and NORÉN (**11**), STILES (**15**), THOMPSON (**16, 17, 18**), and TISON (**22**) on *Saxegothaea* and *Microcachrys*, the group as a whole has become fairly well known. *Pherosphaera*, with two species, is the the only genus as yet untouched, and therefore will not be considered in the following discussion.

One of the chief interests of the family is the question of relationships. The division of the Coniferales into the two families Taxaceae and Pinaceae was made originally on the basis of external characters, but with increasing knowledge of the Podocarpineae certain resemblances to the Araucarineae have been more and more emphasized, until it has even been suggested that these two tribes should form a group by themselves.

Three papers on *Phyllocladus* by Miss ROBERTSON (**13**) and Miss KILDAHL (**8, 9**) are of particular interest because of the difference of opinion in regard to the affinities of that genus. *Phyllocladus* was classed with the Podocarpineae by STRASBURGER, removed to the Taxineae by ENGLER and PRANTL, and finally made a sub-family by itself by PILGER (**12**) in 1906; and now, as its life history is studied, its place is again called in question. MISS ROBERTSON'S work was

chiefly anatomical. Miss KILDAHL'S work was done in this laboratory, and I have had the opportunity of examining her preparations. The receipt of additional material has made it possible to continue the study and to fill in some of the missing stages. This work, a previous study of *Dacrydium*, and the opportunity of examining some material of *Podocarpus* have given occasion for the present paper. I shall first consider *Phyllocladus*, and later take up the larger question of the relationships of the Podocarpineae.

I. Phyllocladus

The material sent by Dr. L. COCKAYNE of Christchurch, New Zealand, consisted of staminate cones collected at intervals of a few days from October 16 to November 13, and ovulate cones of November 8, 13, 25, December 3, 18, 31, January 8, 28. The iron-alum hematoxylin and orange combination was found very satisfactory in staining, as it brought out cytological details remarkably well for tissues killed in formalin and alcohol.

THE MALE GAMETOPHYTE

Miss KILDAHL reports (1) the formation of two prothallial cells, the first of which is usually evanescent; (2) the presence of four, occasionally five, free nuclei in the mature pollen grain; and (3) the division of the body cell into two equal male cells.

My material furnishes a close series, beginning with the microspore stage. The wings are comparatively small and irregular, recalling those of *Microcachrys*, and are formed in the ordinary way as cavities in the exine. The intine is usually rather thin. Very small starch grains occur, but are never conspicuous. Figs. 1–5 show the cutting off of the prothallial cells. The first usually degenerates so quickly that it is hard to find in the older grains. In fig. 4 it is seen partly covered by exine; this is an oblique section escaping the wings and making the spore coats appear uncommonly thick.

The generative cell is formed in the usual way and divides anticlinally, as in the case of *Ginkgo*, *Podocarpus*, and *Dacrydium*, and presumably in all the Podocarpineae. The four-celled stage, as shown in fig. 7, but for the wings might very easily be mistaken for the shedding stage in *Ginkgo*. In the latter, it will be remembered,

the generative cell does not divide until after the tube begins to grow. The spindle in *Phyllocladus* is always more or less oblique, and results in the formation of a larger, more centrally placed body cell and a small stalk cell.

In fig. 13 there is shown a peculiar but very common feature of the sections, the appearance as of an additional cell cut off from the body cell, but without a nucleus. This was noticed also in *Podocarpus* and *Dacrydium*. JEFFREY and CHRYSLER (7), in the case of *Podocarpus ferruginea* and *P. dacrydioides*, describe a second lateral derivative cell and picture it with a nucleus. BROOKS and STILES (1) find the same thing in *P. spinulosa*, but it is not clear whether a nucleus is present or not. It is in these species that the most extensive prothallial tissue is found, consisting of eight cells. In the forms studied by BURLINGAME and myself, as well as in *Dacrydium* and *Phyllocladus*, no nucleus ever appears in the extra section of cytoplasm. The explanation is most easily found in *Phyllocladus*, where horizontal sections show that it is really only a part of the stalk cell. When we consider the shape of the generative cell and the position of the spindle in the division, it is evident that an oblique wall in such a dome-shaped structure could not help resulting in the partial encircling of one cell by the other. The situation can be most clearly shown by diagrams. A horizontal section in the position shown by the dotted line *xy* in fig. 15 would give a view such as is outlined in fig. 16, while fig. 15 is the vertical section through the dotted line in fig. 16. Fig. 17 is an oblique section in about the position of the dotted line *vw* in fig. 15. In this case the second prothallial cell is seen encircled by the stalk cell. A change of focus brings into view the body and tube nuclei and a portion of one wing.

If the stalk nucleus, as shown in fig. 16, were a little more elongated, it would be quite possible to obtain a vertical section in such a position as to show a small part of it on each side of the body cell. The appearance of JEFFREY and CHRYSLER'S and of BROOKS and STILES'S figures of *Podocarpus ferruginea*, *P. dacrydioides*, and *P. spinulosa* suggests this as a possible explanation of the second lateral derivative.

The fact has been noted that the division of the generative cell is anticlinal in Podocarpineae and *Phyllocladus*, and periclinal in other conifers and in cycads, the relative position in the latter having given

rise to the term "stalk cell." It will be remembered that the division takes place in the former before and in the latter after germination has begun. Fig. 18 is a diagram showing this stage in *Dioon*, taken from CHAMBERLAIN (**3**). If in the case of *Phyllocladus* the generative cell should enlarge upward toward the tube before the division, we can easily see that the oblique wall, failing to touch the prothallial cell, would give us the *Dioon* situation. On the other hand, if the wall in *Dioon* were a little lower down or slightly more oblique, we should have a section very like that of *Phyllocladus*. From this point of view the distinction between the anticlinal and periclinal division appears to be related to the time at which the division takes place, and to be of little significance in itself.

Throughout the development of the gametophyte, though distinct cells are formed, each bounded by a *Hautschicht*, there is no evidence of cellulose walls. This I believe to be true also in the *Dacrydium* and *Podocarpus* which I have examined. NORÉN (**11**) fails to find cellulose walls in the case of *Saxegothaea* except in the first prothallial cell, and THOMPSON (**17**) finds them in *Microcachrys* only in the prothallial cells.

Miss KILDAHL mentions the occasional persistence of the first prothallial cell. Figs. 11 and 12 show not only this but also a still more rare case in which the second has divided. This, it will be remembered, is the usual condition in *Dacrydium*, *Microcachrys*, and *Saxegothaea*. In *Dacrydium*, moreover, the first prothallial cell very often degenerates early, which makes the resemblance to *Phyllocladus* still stronger.

As in all the Podocarpineae so far studied, the prothallial and stalk nuclei become free in the general cytoplasm. This may occur in *Phyllocladus* before the grains are shed, but sometimes not until after they reach the micropyle. The mature grain contains the body cell, and the free prothallial, stalk, and tube nuclei.

Young tubes were found in the nucellus November 20. Fig. 19 shows the tube nucleus in advance, followed by the others, and the distinctly organized body cell still in the grain.

My work does not confirm Miss KILDAHL'S in regard to the male cells, as in every case where a complete series of sections was secured, a decided difference in size was evident. The functional

cell is almost always in advance. It has not only more cytoplasm than the other, but nearly always a larger nucleus, and often the other shows signs of degeneration. Figs. 20 and 32 are both drawn so as to show the largest diameter of each male cell and nucleus. The division of the cytoplasm is sometimes hard to demonstrate, and the appearance is that of two free nuclei. Careful staining, however, shows that two definite male cells are formed.

THE FEMALE GAMETOPHYTE

Some belated cones collected November 18 gave the earliest stages. Fig. 21 shows an ovule with its free nucellus, its wide open micropyle with pollen grains, and the arillus making its appearance as a slight swelling at the base. The stony part of the integument develops from a layer two cells deep. The "outer fleshy layer" does not thicken up, but remains represented by only the epidermis and the cells directly under it.

The megaspore mother cell evidently gives rise to a row of three cells, the innermost being the functional megaspore; in fig. 3 it has germinated and has two free nuclei. The young prothallus is surrounded by a layer of glandular, vacuolate cells encroaching on the surrounding nucellar tissue. This "spongy layer" at a later period is much more marked and the cells become binucleate. The megaspore membrane soon appears and is well marked in the early free-nucleate stages. In having the megaspore membrane and spongy layer *Phyllocladus* agrees with all the Podocarpineae except *Podocarpus*, and differs from all the Taxineae.

Wall formation was not found, nor archegonium initials. The development of the young gametophyte is evidently rapid, for material collected November 25 was in the free-nucleate stage, while that of December 3 contained archegonia and an occasional very young embryo.

The gametophyte produces two archegonia, each with its jacket of multinucleate cells; Miss KILDAHL found occasionally three or four. The youngest archegonium obtained is shown in fig. 24. The width at the top seems to be due to the rapid centrifugal growth of the tissues at the upper (archegonial) end of the prothallus, which is indicated by radial lines of cells and numerous spindles. The initial

has divided, forming a central cell and a primary neck cell; the latter gives rise by two divisions to a plate of four cells (figs. 25–27). An exceptional case is seen in fig. 29, where a division has occurred in each of the four cells. Cellulose walls (in this division), however, are not formed, the cells being separated merely by a *Hautschicht*, and in one of them not even a *Hautschicht* appears. The cytoplasm of the central cell is very delicate in the early stages, but gradually thickens up. The nucleus is rather small and lies at the upper end close under the neck.

There is an interesting peculiarity in the neck development of *Phyllocladus* which, so far as I know, has not been reported in any other genus. Miss KILDAHL described the pollen tube as pushing its way into the archegonium with two apparently detached cells in front of it, which she thought were the remains of a crushed neck. Fig. 32 shows this stage, but there are four neck cells, and they are connected with the adjacent jacket cells by a distinct membrane. This membrane at first sight is easily mistaken for the wall of the pollen tube, but the latter is very thin and usually shrinks away from the archegonium in the preparations.

The origin of this peculiar condition is found in a series of earlier stages. The young archegonia are superficial and the necks are covered by the heavy megaspore membrane (figs. 24–26). The pollen tubes at this time come in contact with the prothallus near the necks, and the adjacent tissues grow rapidly, leaving the archegonia at the bottom of considerable cavities which are occupied by the tubes (fig. 36). In *Cephalotaxus*, according to COKER (4), the archegonia, in the absence of pollination, may be entirely inclosed by the growth of the lateral tissue. The megaspore membrane is always a little thinner at the micropylar end, but disappears entirely inside the archegonial cavities (fig. 37), apparently digested by the male gametophyte. Fig. 27 shows it beginning to disappear under the advancing tube. The growth of the female tissues and the pressure of the tube result in a lateral stretching, first of the neck, then of the adjoining jacket cells (fig. 28). The walls of these latter are able to resist the digestive action and enlarge enormously, until just before fertilization they appear as the membrane mentioned above (figs. 33–35).

An interesting situation is shown in fig. 34. The ovule contained

three archegonia, of which the two shown had apparently arisen from adjacent initials and formed a complex with a common jacket. The necks, consisting of four cells each, are attached to one another, one on each side of the common wall. This wall is almost parallel with the plane of the page and passes between the two egg nuclei. In another gametophyte three archegonia were found with a single jacket layer separating two of them; the usual amount of tissue lay between them and the third.

Fig. 33 illustrates the resistance of the jacket membrane to the action of the tube. The neck of this archegonium has been pushed into a vertical position, and part of the egg cytoplasm has been squeezed away from the rest and shows signs of degeneration.

Shortly before fertilization a ventral canal nucleus is cut off, but there is no trace of a wall (figs. 30, 34). In this *Phyllocladus* agrees with *Podocarpus*, *Taxus*, and *Cephalotaxus*, but not with *Torreya*. In the latter not even a nucleus has been found.

Podocarpus is the only member of its tribe whose female gametophyte has been studied. In it COKER (5) found six to ten archegonia. The neck varies greatly, having commonly three tiers of four cells each, but sometimes the number of cells is more than twenty-five.

FERTILIZATION AND THE EMBRYO

At the time of fertilization both egg and jacket cells are rich in "proteid vacuoles," and the egg nucleus is surrounded by a homogenous and very dense layer of cytoplasm. The contents of the pollen tube enter the egg through the neck, leaving the cells intact. Fig. 35 shows both male cells in the egg; the larger fuses with the egg nucleus, some of the cytoplasm apparently contributing to the embryo. Though no trace of the prothallial, stalk, and tube nuclei could be found in this case, it is reasonable to suppose that they entered with the rest of the contents of the tube. In fig. 27 a tube is seen pressing against the side of an archegonium. With further growth probably the wall will be forced into a vertical position, in which case fertilization can take place in the usual way.

Miss KILDAHL reports the formation of at least eight free nuclei in the proembryo, and my material furnishes nothing more. Ovules collected in January had embryos with two cotyledons and long

suspensors. The entire endosperm tissue is multinucleate, a condition which begins to appear while the archegonia are young; it results from the failure of walls to form. In the older endosperm as many as eight nuclei occur in a cell. The megaspore membrane at the fertilization period is about 2.5 μ thick at the lower part of the prothallus, and about 4.5 μ when the cotyledons appear (fig. 31).

Before discussing relationships, it will be helpful to summarize the important facts about *Phyllocladus*, including the work of Miss ROBERTSON and Miss KILDAHL.

SUMMARY

1. The stamen bears two abaxial sporangia.
2. The pollen grains have two wings.
3. In the male gametophyte there are two prothallial cells; the first usually disappears, the second occasionally divides.
4. The generative cell divides anticlinally but obliquely, and the stalk cell partially encircles the second prothallial and body cells.
5. The mature pollen grain contains the body cell and the free stalk, prothallial, and tube nuclei.
6. There are two unequal male cells, only the larger of which functions.
7. The ovulate structure is a strobilus with a single erect ovule in the axil of each scale.
8. A symmetrical arillus originates from the base of the ovule and remains free from the integument.
9. The outer fleshy layer is represented by two layers of cells.
10. The nucellus is free to the base.
11. The megaspore mother cell gives rise to a row of three cells, the innermost of which is the functioning megaspore.
12. The spongy layer and megaspore membrane are strongly developed.
13. Each ovule contains two archegonia, occasionally three or four, each with its own jacket, but sometimes there is a complex of two in a common jacket.
14. The neck of the archegonium consists of four cells in a plate; occasionally these divide anticlinally.
15. There is a ventral canal nucleus.

16. The mature archegonium is very wide at the top and is covered by a membrane formed from the walls of the adjacent jacket cells.

17. In fertilization the contents of the pollen tube pass through the neck, leaving it intact.

18. Some male cytoplasm contributes to the embryo.

19. There are at least eight free nuclei in the proembryo.

20. The embryo has two cotyledons and a very long suspensor.

21. Mesarch bundles occur in the cladodes.

22. Taxinean sculpturing is found in the tracheids.

23. No vascular strands enter the ovule; the ovular supply consists of two strands facing each other and ending in a tracheal plate below the integument.

DISCUSSION

The characters which point toward the affinity of *Phyllocladus* with the Taxineae are: (1) the structure of the ovule, (2) the symmetrical arillus, (3) resemblances of the ovulate cone to that of *Cephalotaxus*, (4) mesarch bundles, and (5) taxinean sculpturing of tracheids. Characters indicating a relationship with the Podocarpineae are: (1) the character of the male gametophyte, (2) the structure of the stamen, (3) winged pollen grains, (4) megaspore membrane and spongy tissue.

The first point is perhaps the strongest argument for taxad affinity, as the erect, free, axillary ovule is characteristic of the whole group. This ovule, however, is a primitive type which we would expect to find at the base of any line. Though the progress of the podocarps has been toward inversion and fusion of parts, which finds its highest expression in *Podocarpus* itself, we find many relatively primitive stages represented. In *Dacrydium*, *Saxegothaea*, and *Microcachrys* the ovule is free from the scale and epimatium, except at the base, and in the various species of *Dacrydium* we find all positions from erect to completely inverted. The young ovule of *Saxegothaea* is in early stages perpendicular to the scale and becomes inverted only as the result of later growth. This, together with its position near the base of the scale, is suggestive of ancestors with erect, axillary ovules.

The homology of the symmetrical arillus which originates from

the base of the ovule, and of the one-sided epimatium arising from the scale is uncertain. The origin of the latter may be related, however, to the foliar origin of the ovules, and, as Miss ROBERTSON states, "the asymmetry is correlated with the inverted position of the ovule, so that it will not do to lay too much stress on this point, as proving that epimatium and arillus are not homologous."

Though the external resemblance between the cones of *Phyllocladus* and *Cephalotaxus* is rather striking and the vascular supply is the same, this may merely point back to a common origin of all the Taxineae. *Cephalotaxus*, moreover, has two ovules in the axil of each bract, while *Phyllocladus* agrees with the Podocarpineae in having only one.

The presence of mesarch wood in the cladodes owes its significance to the fact that mesarch wood is more common in Taxineae than in any other group of conifers. This, too, is an ancestral character, for which we would look in the primitive members of any group. STILES finds it in the ovular supply in *Saxegothaea*, whose cone is regarded as the most primitive of the podocarps.

Taxinean sculpturing of tracheids, too, would be more significant if it were confined to Taxineae, but this is by no means true. Such characters as these last two are valuable in connection with other evidence, but have little weight in themselves.

The most convincing evidence of podocarp affinity lies in the entire behavior of the male gametophyte: the formation of prothallial tissue, the freeing of the nuclei, and the early division of the generative cell. The presence or absence of prothallial cells is a definite group character; where they occur at all they are characteristic of an entire family, and where absent in one member they are lacking in all. Permanent prothallial cells are known nowhere in conifers except in Podocarpineae and Araucarineae; and the early division of the generative cell, which characterizes the former, occurs nowhere else except perhaps in araucarians. Prothallial tissue is a primitive character, possessed, as we presume, by the ancestors of all conifers; but the Taxineae have eliminated it entirely, while it still remains one of the most characteristic features of the Podocarpineae.

The morphology of the different forms of stamen in the conifers is an open question. The Taxineae, according to COULTER and

LAND (**6**), are reducing the epaulette type of *Taxus*, while no other family, except araucarians, has a stamen with more than two pollen sacs. If the two types have a common origin, only the *Taxus* stamen can be the primitive one; and in this case *Phyllocladus* has gone a long way in the podocarp line of development. A different origin, of course, would remove *Phyllocladus* still farther from Taxineae.

Winged pollen is entirely absent among the Taxineae, but is characteristic of the Podocarpineae, being absent only in the *Saxegothaea*. The irregularity in size and number of the wings in *Microcachrys* has given rise to THOMPSON'S (**16, 17**) theory that the two-winged condition has developed within the group and shows no relation to Abietineae. This gives us another podocarp line along which *Phyllocladus* has advanced.

THOMPSON (**20**) lays a good deal of stress on the megaspore membrane as a primitive character. It is entirely eliminated in Taxineae, but characterizes all the members of the other family except *Podocarpus* itself. As the ovulate structures of the type genus are by far the most specialized of the family, this is not surprising. Miss ROBERTSON thought the megaspore membrane and spongy tissue were in some way correlated with the presence of winged pollen, but their occurrence in *Saxegothaea* with its wingless microspores breaks down this supposition.

CONCLUSION

When we consider the question of relationships, it is evident on the whole that: (1) *Phyllocladus* has primitive characters of the Taxineae which are being eliminated in the Podocarpineae; (2) it has primitive characters of the Podocarpineae which have been entirely eliminated in the Taxineae; (3) it has some advanced characters of Podocarpineae; (4) the taxad resemblances are on the whole more superficial and variable, and the podocarp features more fundamental; (5) the resemblances to Podocarpineae are too strong to justify the retention of the intermediate family.

We conclude, therefore, that *Phyllocladus* is a relatively primitive member of the Podocarpineae, which branched off from them a comparatively short time after their separation from Taxineae. Whether the two families form a distinct line from other conifers is not at all involved in this conclusion.

II. Podocarpineae and Araucarineae

The more important contrasts between the araucarian and podocarp lines are in the structure of the stamen and ovulate strobilus, and in the method of fertilization. The araucarian stamen is a comparatively primitive type and is somewhat suggestive of *Ginkgo*. It is one-sided and bears three to thirty pendent pollen sacs; while all the genera of the Podocarpineae, as before mentioned, have the microsporangia definitely reduced to two.

The ovulate cone in Araucarineae is a compact structure with many scales, ripening dry; while the podocarp line is characterized by the reduction in the number and size of cone scales and the tendency to fleshy development. *Saxegothaea*, the form which stands nearest the araucarians, shows the least amount of reduction in both size and number of scales; *Microcachrys* is next; while in other forms the cone is represented by the single, apparently terminal, ovule and a few rudimentary scales. The podocarp ovules have the arillus, or epimatium, which is absent in araucarians. The cone scale of *Araucaria*, on the other hand, bears the so-called ligule, represented in *Agathis* by only a slight projection from the surface. The ovules of *Saxegothaea* are united with the scale only at the base, while in *Araucaria* they are described as imbedded in the tissues of the scale. In *Agathis*, however, the ovules are free and the seeds winged.

The female gametophyte is too little known in either group for any adequate comparison. That of the Araucarineae, however, is apparently much more primitive than that of the known podocarps. The archegonia are very numerous and are described (SEWARD and FORD **14**) as situated at the bottom of deep pits and usually not connected with the surface by necks. Investigation is needed here to show whether they are really hypodermal, or whether the condition is brought about by overgrowth of adjacent tissue in the development of a neck so massive as not to have been recognized. The position of the ovule of Araucarineae in the tissues of the scale is another subject which needs interpretation.

Fertilization in Araucarineae (THOMPSON **19**) is angiosperm-like, in that the pollen does not reach the ovule, the tubes growing over the surface of the scales to reach the micropyle.

The first suggestion of relationship between the two groups came from the study of the male gametophyte. This has recently been supplemented by studies of *Saxegothaea*, which have brought out striking resemblances to certain species of araucarians. The geographic distribution is also suggestive of alliance between these two great southern groups.

THE MALE GAMETOPHYTE

In the Araucarineae, as in the Podocarpineae, there are two original prothallial cells, from which by subsequent divisions a more or less extensive tissue is formed. In Araucarineae there may be as many as thirty cells (LOPRIORE **10**; THOMPSON **21**). JEFFREY and CHRYSLER (**7**) found an apparently mature pollen grain of *Agathis australis* with a prothallial complex of eight cells, which is the situation in some species of *Podocarpus*. Other species of *Podocarpus* have four cells, resulting from a single division of each original prothallial cell. In *Dacrydium*, *Saxegothaea*, and *Microcachrys* there are two to four permanent prothallial cells, in *Phyllocladus* one to three. Thus we have a complete overlapping prothallial reduction series from *Agathis* to *Phyllocladus*.

The generative cell is found in Araucarineae as in the others, but the division into stalk and body cell has not been observed. Unless this division takes place in the tube, as is true of most conifers, it must either have been eliminated or missed in the preparations. The otherwise close correspondence with the gametophyte of Podocarpineae inclines one toward the latter supposition. Further work is needed on this point.

THE OVULE AND FEMALE GAMETOPHYTE

The single inverted ovule is characteristic of both families. The inversion was probably developed independently, however, in the two lines. In *Saxegothaea*, as has been said before, the young ovule changes from an erect to an inverted position in the course of its development. The free nucellus of *Dacrydium* and *Phyllocladus* is a primitive feature which they have in common with araucarians.

The female gametophyte, as before stated, is little known. A

point of resemblance, however, between Araucarineae, *Phyllocladus*, and *Podocarpus* is found in the cutting off of the ventral canal nucleus in the archegonium.

SAXEGOTHAEA

The resemblance of *Saxegothaea* to the araucarians, noted by STILES (15), NORÉN (11), THOMPSON (18), and TISON (22), consists chiefly of anatomical characters and certain external features of the cones. STILES finds in the stem tracheids somewhat araucarian in character, "an occasional tendency to a two-ranked arrangement of the pits, and in these cases the pits become alternate and hexagonal." Two-ranked and alternate pits horizontally flattened have also been found in *Dacrydium*. The prominence of transfusion tissue is another character suggestive of araucarian affinity.

The staminate cone is described by STILES as somewhat araucarian in general appearance, and the wall of the microsporangium as strikingly like that of *Araucaria Rulei*. BROOKS and STILES (1), in their study of *Podocarpus spinulosa*, state that the wall of the sporangium is very like that of *Saxegothaea* and *Araucaria*. Wingless pollen is another point of contact. The fact that the pollen grains of all the other Podocarpineae have wings does not affect the argument, if we accept THOMPSON'S theory that they were developed within the group (15, 16).

In the ovulate cones of both *Saxegothaea* and *Araucaria*, especially *A. Rulei*, there is a gradual transition from foliage leaves to sporophylls. This and the similarity in the vascular anatomy are considered by THOMPSON and TISON as indications of the simple nature of the strobilus in these groups. The occurrence of a single resin duct in the sporophyll is, according to STILES, another indication of this in *Saxegothaea*.

One of the most striking features of *Saxegothaea* is the projection of the nucellar tissue through the micropyle, where it expands to form a stigma-like knob. The same thing occurs less conspicuously in Araucarineae, but, with the exception of a few abnormal cases in angiosperms, is elsewhere unknown. This feature appears to be related physiologically to the difficulty of fertilization, and its morphological significance is doubtful. THOMPSON (19) sees in it a

tendency toward protosiphonogamic fertilization, significant in relating *Saxegothaea* to the araucarians.

A good deal of stress has been laid recently on the distribution of the vascular bundles in the ovulate sporophylls. STILES finds the branching in *Saxegothaea* very similar in the main to *Araucaria Rulei* and *A. Cookei*, and the arrangement in *Microcachrys*, though not unlike that of *Saxegothaea*, resembles more closely *A. Bidwillii*. TISON agrees essentially with STILES in regard to the details in *Saxegothaea*, but finds greater resemblance to *A. brasiliana* and *A. imbricata*.

RESULTS

STILES, NORÉN, THOMPSON, and TISON all agree in the relationship of the two groups, the intermediate position of *Saxegothaea*, and the simple structure of the ovulate scale in the two families, but they differ somewhat in the application of their results. STILES says: "While we must wait for fuller knowledge before making any definite statement, it would appear that these two orders of Coniferales are descended from some common ancestor with its micro- and megasporophylls both arranged spirally in cones. Along one line of descent we find the Araucarieae, along the other is *Saxegothaea* leading on to *Microcachrys* and the other Podocarpeae." NORÉN comes to the same conclusion, regarding *Saxegothaea* as nearest to the Araucarineae, but unquestionably a member of the Podocarpineae; but TISON considers it more closely related to the latter group, and regards *Microcachrys* as the connecting link.

But it is the attempt to homologize the ovulate structures of conifers that has given rise to the greatest amount of discussion. In conifers with foliar ovules, as is well known, there is more or less completely represented a double system of bundles, that from which the ovule gets its supply being inverse to the other. The two systems may originate separately from the axis, or the one supplying the ovule may arise at various situations from the other. The former varies also in extent, from a considerably branched system to one or two weakly differentiated bundles.

WORSDELL (**23**) in 1899 made a study of the distribution of the vascular bundles in various conifers, and in 1900 (**24**) published a

very complete historical account of the controversy on the morphology of the ovulate cone. He agrees with ČELAKOVSKÝ that the arillus of Taxaceae, the ligule of *Araucaria*, and the ovuliferous scale of the other Pinaceae are homologous and are all a second integument, that all the ovulate cones are morphologically compound, but that the sporophyll is suppressed and represented by the ovule alone.

THOMPSON (18) in 1909 brought out some interesting data in regard to the inversion and its relation to the theory of the axillary shoot. The inversion of the bundles supplying the ovule he explains as normal for sporangial supply, and cites cases of such inversion in the microsporophylls of cycads and of some conifers. In *Tsuga* he found two inversions, the ovular supply being inverse to that of the scale, which in turn is inverse to that of the bract. The first inversion he considers as homologous with that of the scale of *Saxegothaea* and related to the ovule, while the second may be explained by the theory of the compound nature of the sporophyll. On this basis he makes two groups of conifers, the Araucarineae and Podocarpineae having simple strobili and ovules on the morphological upper surface of the scale, and the other Pinaceae having compound strobili and ovules morphologically abaxial.

TISON regards the arillus of *Saxegothaea* and the ligule of *Araucaria* as homologous with the ovuliferous scale of other conifers, calling them an ovuliferous appendage. He does not commit himself in regard to the axillary shoot theory as affecting Abietineae, Cupressineae, and Taxodineae, but agrees with THOMPSON that the cones of *Saxegothaea*, Podocarpineae, and Araucarineae are simple. He favors the inclusion of *Saxegothaea* and Podocarpineae in the Araucariales suggested by SEWARD and FORD (14).

CONCLUSION

After reviewing the whole situation, one is impressed with the fact that both Podocarpineae and Araucarineae are very primitive, that they are probably related, but that the question is by no means settled. The whole coniter group still appears as a maze of cross resemblances. If we confine ourselves to one or two characters, the problems of relationship are comparatively simple, but bring more into consideration, and we are immediately in trouble. The

relation of the podocarps with Araucarineae on the one hand, for instance, is complicated with evidence of connection through *Phyllocladus* with taxads on the other; and the two last-named tribes are apparently very widely separated from one another. It is true that the evidence for the first relation is the stronger, for without *Phyllocladus* the question of taxad affinity would hardly be raised at all; while without *Saxegothaea* we should still have much evidence of the other connection. The existence of *Phyllocladus*, however, cannot be disregraded.

On the other hand, the argument for araucarian connection lacks conclusiveness. In the first place, it is based largely on primitive characters. These may indicate merely that neither group has advanced far from the original ancestral conifer stock. The two lines may be quite distinct and both short. Two short branches from the same trunk may have their ends nearer together than two twigs of the same long branch. Most of the remaining evidence depends upon the external features of the cones and the distribution of vascular bundles. Such evidence is unsatisfactory on account of the great variability of the structures concerned. Great variations are found between closely related forms. *Araucaria* with its ligule and apparently imbedded ovule, and *Agathis* with its free winged seed, or the ovulate structures of different species of *Dacrydium*, are examples. TISON finds variations in the arrangement of the vascular bundles of *Saxegothaea*, not only in different individuals, but in the same plant. He says: "En ce qui concerne les écailles fertiles, je dois tout d'abord faire remarquer que la disposition du système fasciculaire à leur base, dans la région ovulifère, est très variable souvent dans un même cône, ces variantes n'étant pas nécessairement en rapport avec la position des bractées sur les cônes."

The fact of variability makes it easy to imagine the derivation of a structure from one unlike it in appearance, as the arillus and ligule or ovuliferous scale; but on the other hand, their independent origin becomes equally simple, and one is inclined to doubt the morphological need of such homologies. It may be that the conflicting lines of resemblance among conifers point to a more ancient lineage for all the families than we are apt to think, and in this case the significance of variable features becomes still less.

The greatest gap in our present knowledge of conifers is shown by the Araucarineae. Even in the male gametophyte, which supplies perhaps the strongest argument in the above discussion, a good deal of work is needed. The female gametophyte is little known and the embryo practically not at all. Beside this, we should know the early development of the ovulate strobilus for a proper understanding of the morphology of its parts. In the Podocarpineae we lack adequate knowledge of the female gametophyte, embryo, and development of ovulate structures. Until further data on these points are available, we should be hardly justified in coming to a definite decision in regard to relationships, and at present it seems best to hold Taxineae, Podocarpineae, and Araucarineae apart as separate tribes, leaving open the question of larger groupings among conifers.

Grateful acknowledgments are due to Professors J. M. COULTER and C. J. CHAMBERLAIN, under whose direction this work was done.

THE UNIVERSITY OF CHICAGO

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EXPLANATION OF PLATES IV–VI

Zeiss compensating oculars 4 and 6 mm. and Bausch and Lomb objectives $\frac{1}{8}$, $\frac{1}{12}$, and $\frac{1}{18}$ mm. were used. All drawings, except figs. 15, 16, and 18, were made with the aid of the camera lucida. The magnifications refer to the figures as they appear on the plates, after having been reduced one-half in reproduction.

Abbreviations: p_1, first prothallial cell; p_2, second prothallial cell; *g*, generative cell; *s*, stalk cell; *b*, body cell; *t*, tube nucleus; *a*, arillus; *n*, neck; m_1, functioning male cell; m_2, functionless male cell; *vn*, ventral canal nucleus; *e*, egg nucleus; *m*, megaspore membrane; *sp*, spongy tissue.

FIG. 1.—Microspore. ×950.

FIG. 2.—Spindle for the first prothallial cell. ×950.

FIG. 3.—First prothallial cell cut off. ×950.

FIG. 4.—Spindle for the second prothallial cell; first prothallial cell partly covered by intine. ×950.

FIG. 5.—Second prothallial cell cut off, the first degenerating. ×950.

FIG. 6.—Spindle for generative cell. ×950.

FIG. 7.—Tube nucleus, generative cell, and prothallial cells. ×950.

FIGS. 8, 9.—Generative cell dividing. ×950.

FIG. 10.—Mature pollen grain. ×950.

FIGS. 11, 12.—First prothallial cell persistent and the second divided. ×950.

FIG. 13.—Mature grain, showing a part of the stalk cell on each side of the body cell. ×950.

FIG. 14.—Nuclei becoming free. ×950.

FIG. 15.—Diagram of vertical section through dotted line in fig. 16.

FIG. 16.—Diagram of horizontal section through dotted line *xy* of fig. 15, showing form of stalk cell.

FIG. 17.—Horizontal section, showing stalk and second prothallial cells and tube and body nuclei. ×950.

FIG. 18.—Outline drawing of *Dioon*.—From CHAMBERLAIN.

FIG. 19.—Body cell in the grain; stalk, tube, and prothallial nuclei in the tube. ×440.

FIG. 20.—Body cell divided, forming two unequal male cells. ×440.

FIG. 21.—Longitudinal section of ovule and bract; pollen grains on the nucellus. ×45.

FIG. 22.—Young stage of the arillus; detail of fig. 21. ×440.

FIG. 23.—Two-nucleate stage of female gametophyte; detail of fig. 21. ×440.

FIG. 24.—Young archegonium, showing primary neck and central cells. ×440.

FIG. 25.—Young archegonium; primary neck cell divided. ×440.

FIG. 26.—A neck cell dividing. ×440.

FIG. 27.—Four-celled neck; megaspore membrane disappearing before advancing pollen tube; the space between the membrane and neck cells is due to shrinkage. ×440.

FIG. 28.—Stretching of adjacent jacket cells under pressure of the pollen tube; body cell and central nucleus not yet divided. ×440.

FIG. 29.—Eight-celled neck. ×440.

FIG. 30.—Egg and ventral canal nucleus. ×440.

FIG. 31.—Endosperm cells and megaspore membrane; January 28. ×950.

FIG. 32.—Egg ready for fertilization; four-celled neck and jacket membrane; male cells, stalk, prothallial, and tube nuclei. ×440.

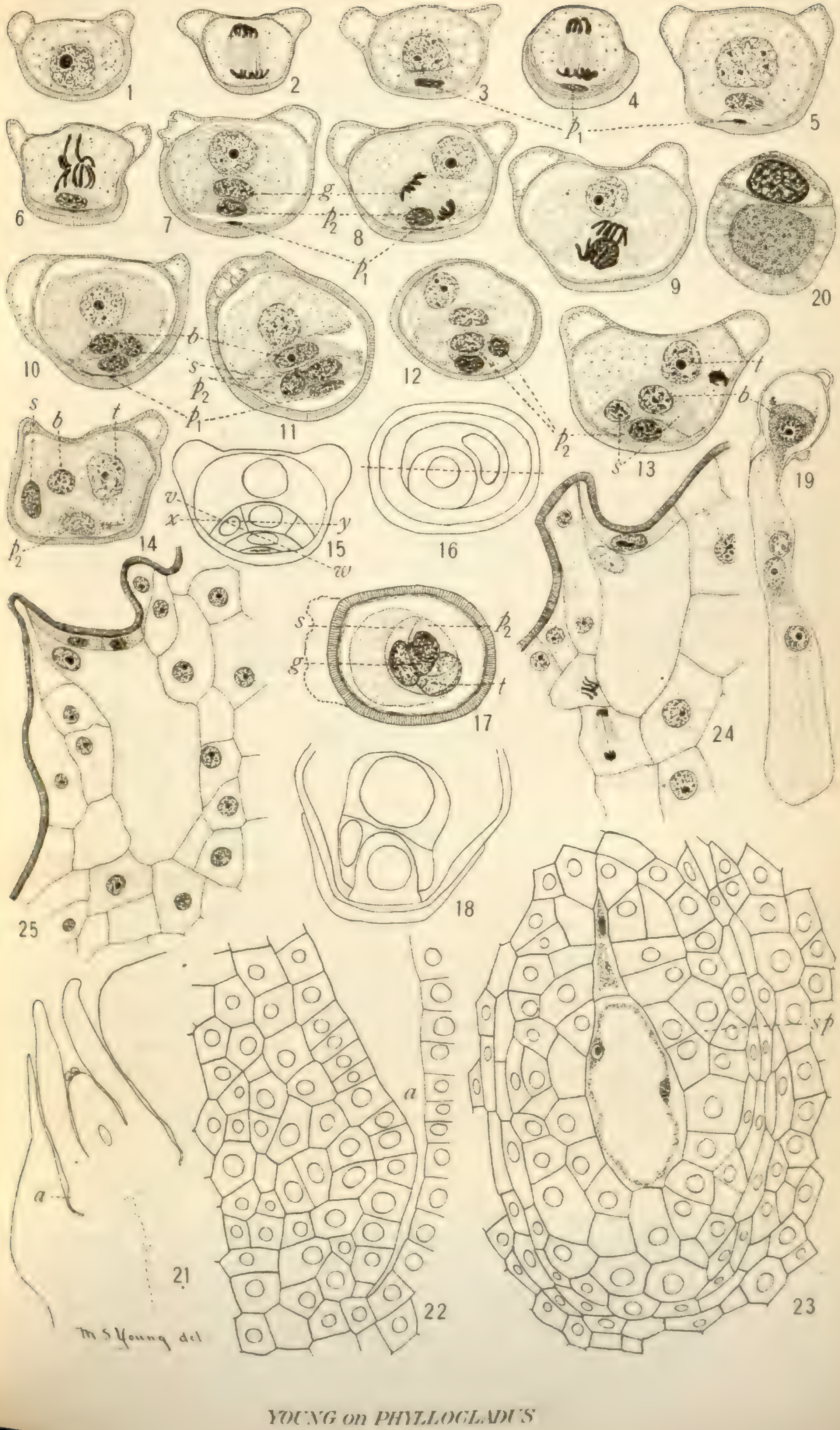
FIG. 33.—Effect of pollen tube on an archegonium; the membrane intact. ×440.

FIG. 34.—Two archegonia in a common jacket; two pollen tubes. ×340.

FIG. 35.—Fertilization. ×440.

FIG. 36.—Female gametophyte. ×45.

FIG. 37.—Megaspore membrane and archegonial cavities. ×440.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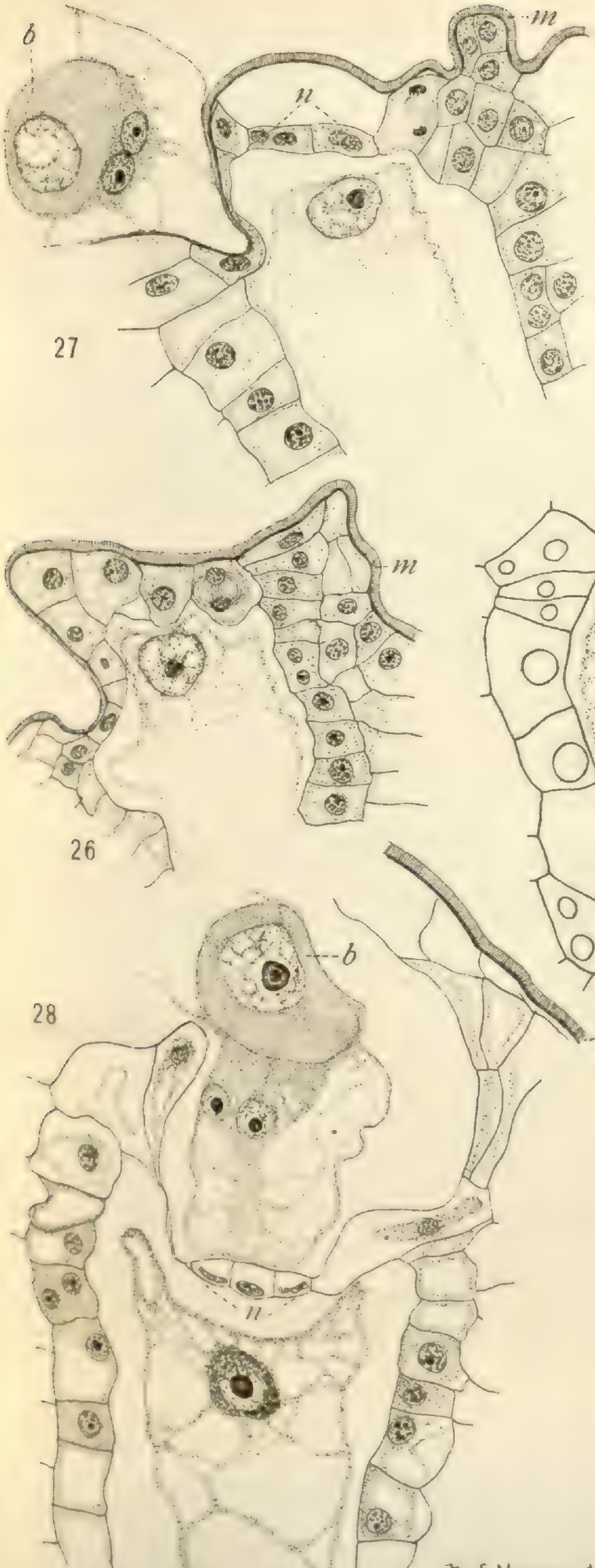

YOUNG on PHYLLOGLADUS

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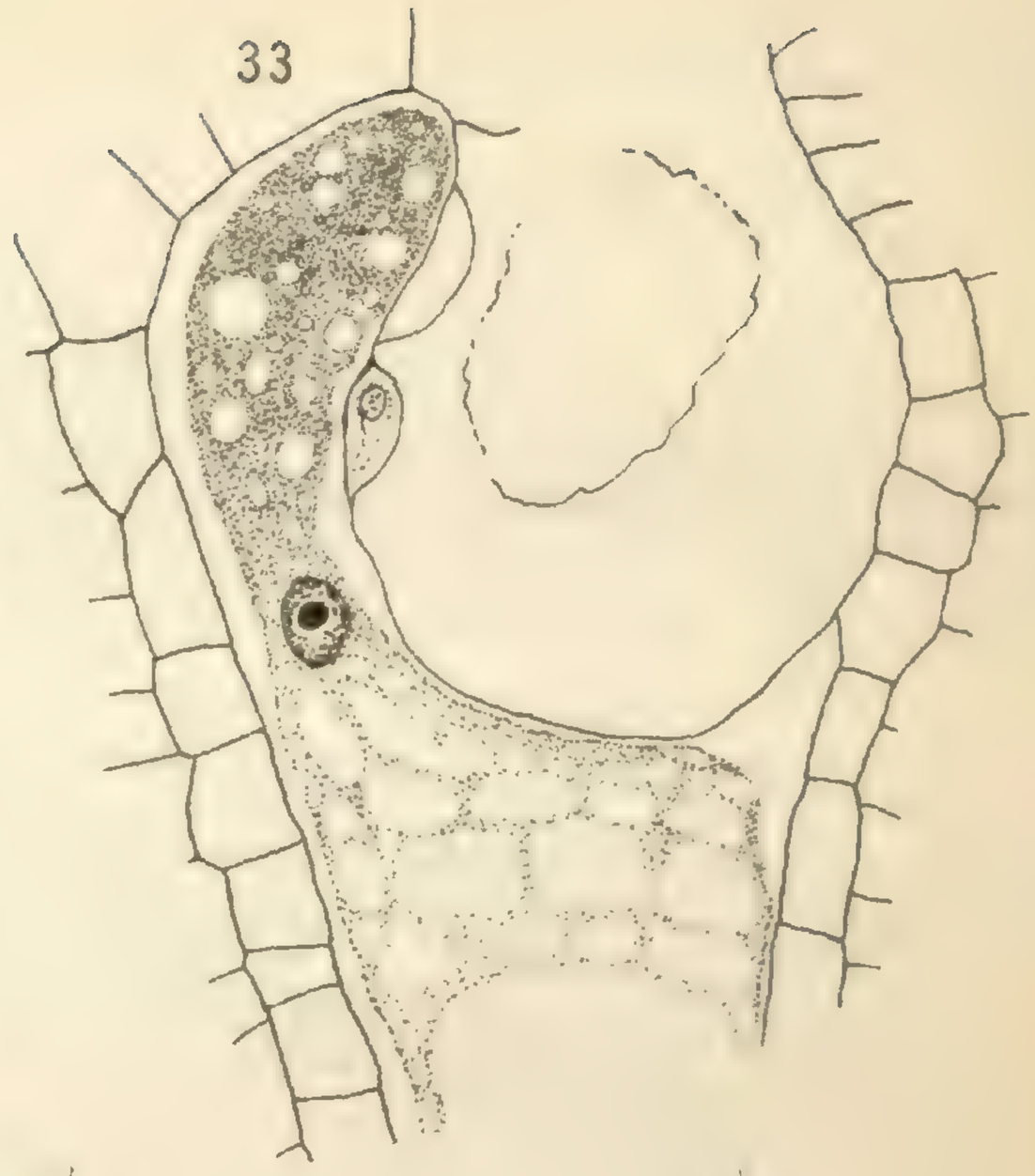

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THE ORIGIN OF RAY TRACHEIDS IN THE CONIFERAE

W. P. THOMPSON

(WITH SIXTEEN FIGURES)

Considerable attention has been devoted in recent years to the phylogenetic significance of ray tracheids in the Coniferae. PENHALLOW (1), arguing from their distribution and from his theory of their origin, concludes that the number in a given species is in direct proportion to its specialization, and that the forms where they are most numerous are derived from those where they are not so well developed. JEFFREY (2), on the other hand, from a study of certain traumatic phenomena, considers that the forms where they attain their greatest development, namely the pines, are the most ancestral, and have given rise by degeneration to the ones in which they occur sporadically. Apart from its intrinsic interest, it is hoped that the present study, by determining the origin of the ray tracheid, will supply a basis for its correct phylogenetic interpretation.

In carrying on the study, a thorough investigation was made of the character and mode of formation of the ray tracheid throughout the individual plant, but more especially in the primitive regions: seedling stem and root, young branch and young root of the adult, and the axis of the seed cone. The forms chosen for detailed investigation were our indigenous species of the hard and soft pines, *Pinus resinosa* and *P. Strobus*, but the results were confirmed in many other forms. The usual method was to follow a ray by means of a series of sections, from its beginning at the pith through the wood to the cambium.

The origin of the medullary ray at the pith has been described and figured by KNY (3) for *Pinus silvestris*. He states that in this region all the ray cells are parenchymatous, and elongated not radially but vertically. These long cells are often in connection with similar cells from rays lying above or below. Very soon they separate, shorten in the vertical direction, and elongate radially to form the typical medullary rays, which during their further course are separate. A later

writer, CONWENTZ (4), agrees with this description and extends it to include the root. I have found the observations of both writers to be practically true for *Pinus Strobus* and *P. resinosa*. In view of what is to follow, however, dissent must be expressed from the statement that during their further course the rays are separate. An important feature which neither writer emphasizes is that the rays in this young wood are low, rarely more than two cells in height.

The further course of the rays in root, stem, and cone axis shows essential differences; accordingly these regions are treated separately.

Root

Some distance from the pith certain peculiar tracheids appear, which KNY and other investigators seem to have overlooked.

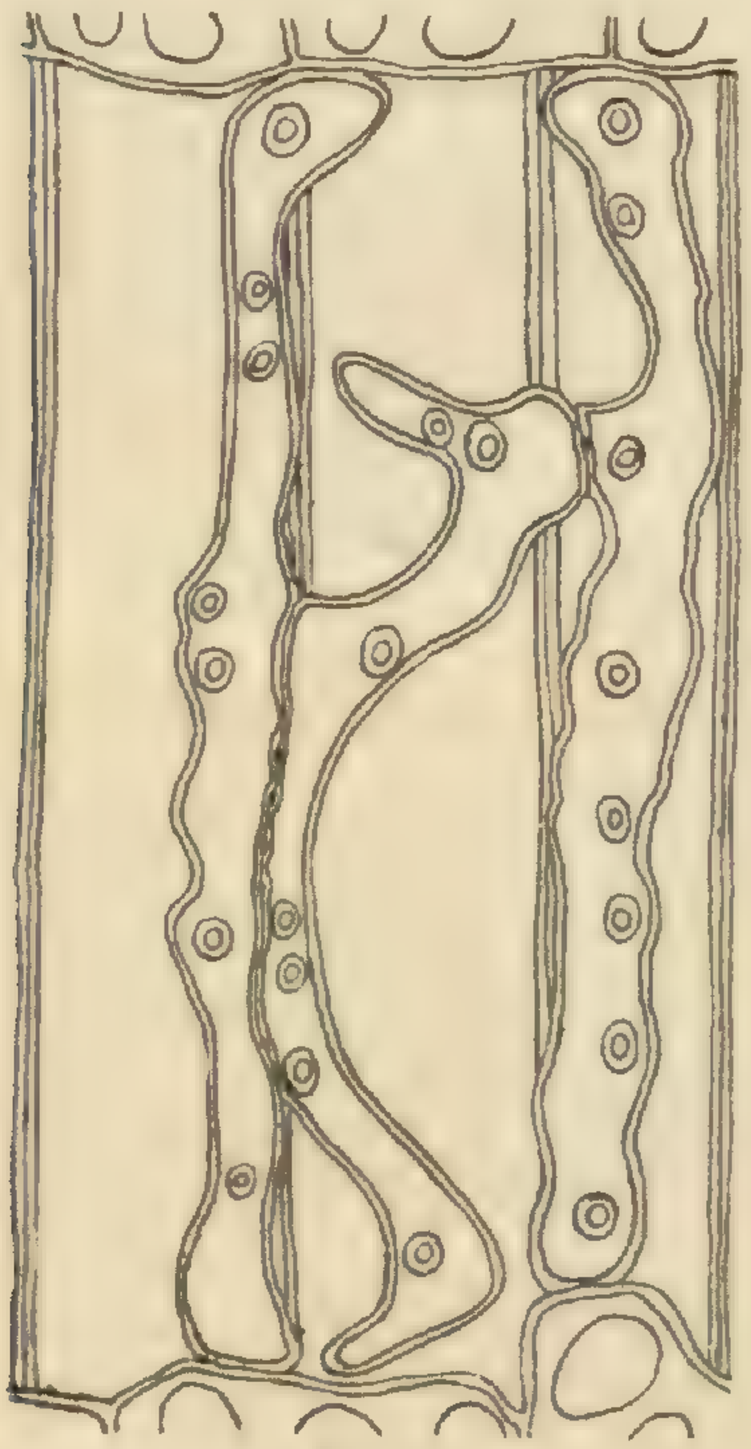

FIG. 1

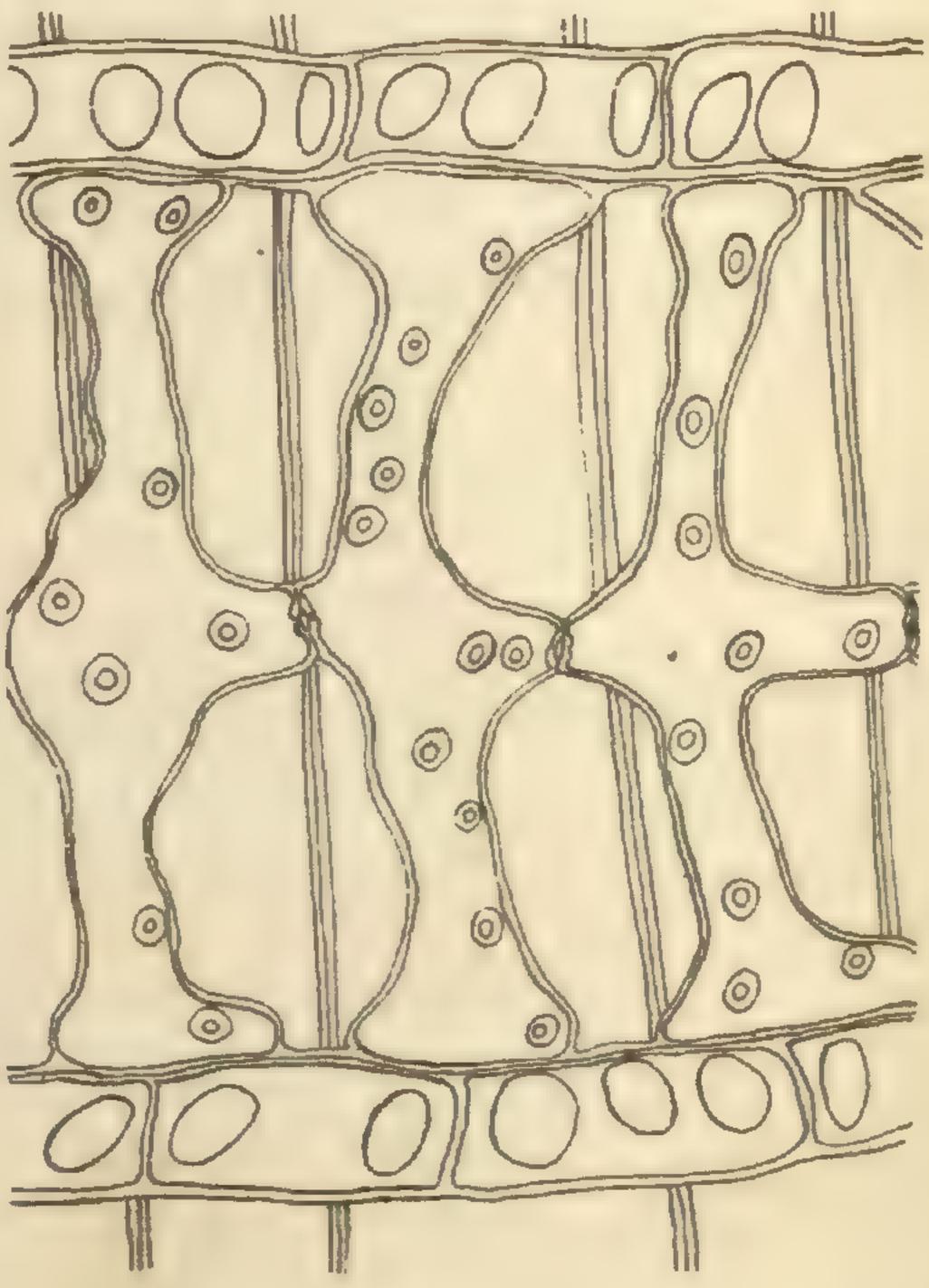

FIG. 2

FIGS. 1, 2.—Fig. 1, *P. resinosa:* young root; short tracheids extending between two rays; fig. 2, *P. Strobus:* young root; short tracheids with characteristic radial projections.

Examples of them are shown in figs. 1 and 2. They occur in radial rows, extending between two rays which lie in the same vertical plane. Consequently they are of various lengths, depending on the distance between the rays. Their form is also variable, often being quite uniform, like tracheids (fig. 1), often very irregular in outline.

A frequent peculiarity is the possession of arms (fig. 2) projecting radially either from the ends, or the middle, or from both, and meeting similar projections from their fellows. In this case the bodies of the cells are some distance apart. The walls of all these short tracheids are generally thinner, and their bordered pits much smaller than those of ordinary tracheids.

The usual sequence of these cells and their transformations toward the cambium are illustrated in fig. 3, which is a camera lucida drawing of two consecutive sections from a series of the root of *Pinus resinosa*. The cambium in this figure is toward the right (this orientation has been preserved throughout my illustrations). On their first appearance, toward the left of the figure, these tracheids have the more regular form approximating ordinary tracheids. Farther out they become irregular, usually with the above mentioned projections; then divisions occur, forming two superposed rows. These soon separate, taking up their position along the rays (center of figure) and forming irregular marginal cells, which gradually become regular and assume the form of true ray tracheids. In the ray at the bottom of the figure, ray tracheids have already been formed, but in one at the top this process has not yet been completed. In *Pinus Strobus* the sequence is similar. Often in both, the series is not so regular as the one just described; some stages may be hurried over, some greatly prolonged. In the one drawn, the transformation has taken place much more quickly than is usually the case, for the transitional stages may often be traced through several years' growth.

That these elements are indeed transitional is further shown in fig. 3 (*Pinus resinosa*) by the development on their walls of the dentations characteristic of the ray tracheids of the hard pines. When they first appear the elements are quite smooth, but as they assume more the shape and character of ray tracheids they acquire these dentations. One may often find intermediate cells whose walls are partly smooth like tracheids and partly dentate like ray tracheids (center of fig. 3).

It is evident that in the root of these forms we have a complete transition between short tracheids and ray tracheids; that by a process of division, of shortening, and of radial extension marginal ray tracheids have been produced from tracheary tissue.

The description so far has dealt with the marginal ray tracheids. The interspersed ones appear about the same time; their origin is illustrated in fig. 4. At the left of the figure are the irregular short tracheids extending between two rays. Farther to the left, that is, nearer the pith, these rays are more distant and the transitional tracheids are longer. To the right the rays gradually approach and

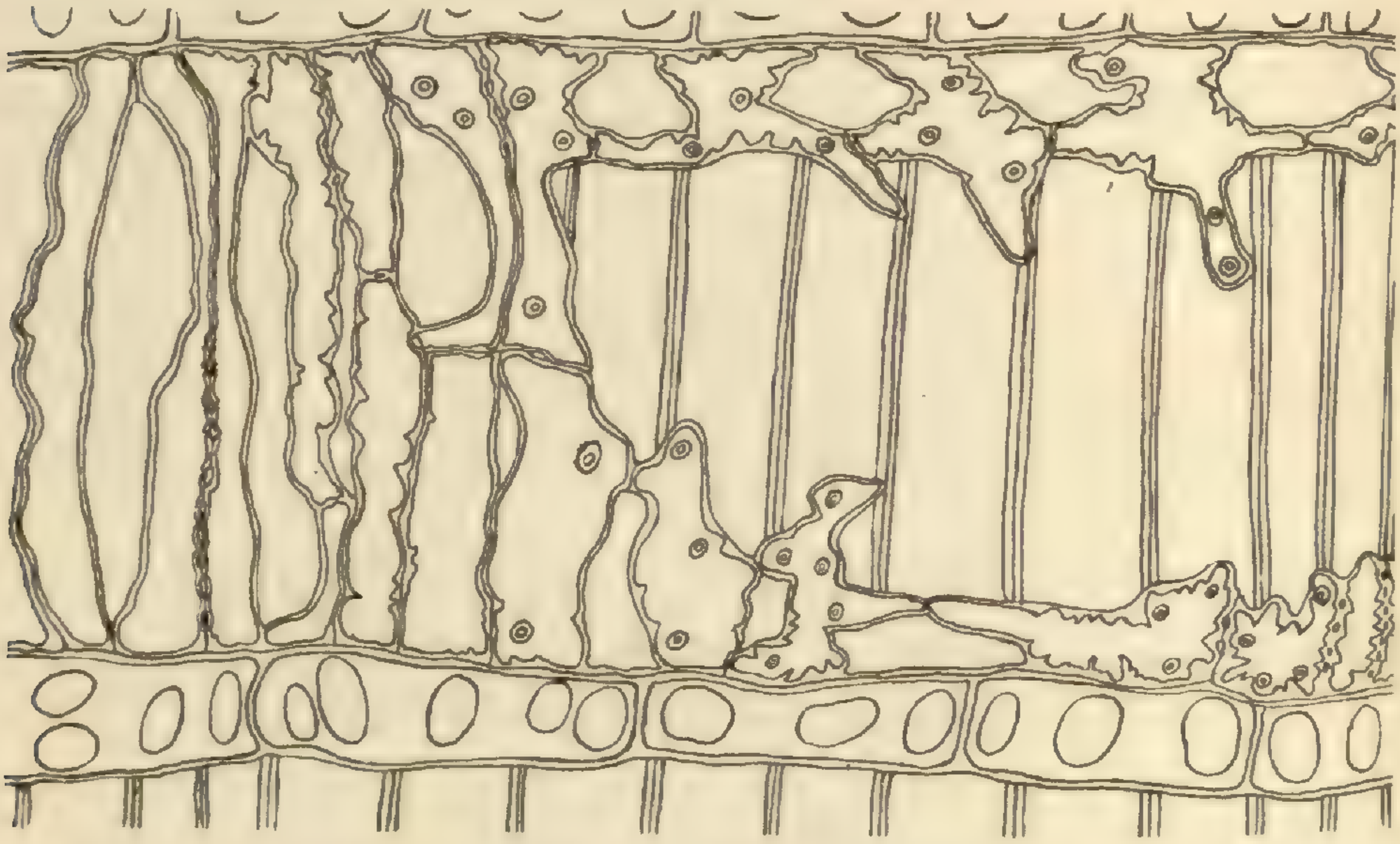

FIG. 3.—*P. resinosa:* young root; the transformation of short tracheids to marginal ray tracheids.

the tracheids shorten to form the regular interspersed ray tracheids which continue to the cambium. Thus interspersed ray tracheids originate from the same kind of tracheary element as the marginal ones. In the latter case the rays separate and the tracheids form along their margin. In the former, the rays draw together and the tracheids shorten and take their place in the center of the resulting composite ray.

The formation of this ray calls attention to an undescribed phenomenon apparently rather common in *Pinus*, namely the fusion of rays. As noted above, when the rays originate at the pith they are usually only one or two cells in height; but in the adult wood many of them are much higher. In the root wood up to twelve years old, careful observations were made to determine to what extent the increased height was due to fusion. This was done by following the rays in a series of sections from the cambium to the pith. It was found that

practically every one of the high rays was formed by a combination of two or more lower ones. Only very rarely was a height of four cells attained otherwise. The so-called *primary* rays are then really formed *secondarily*, by fusion. To what extent this fusion is characteristic of the other forms has not yet been determined, but it would seem that the low ray is the primitive condition in the pines.

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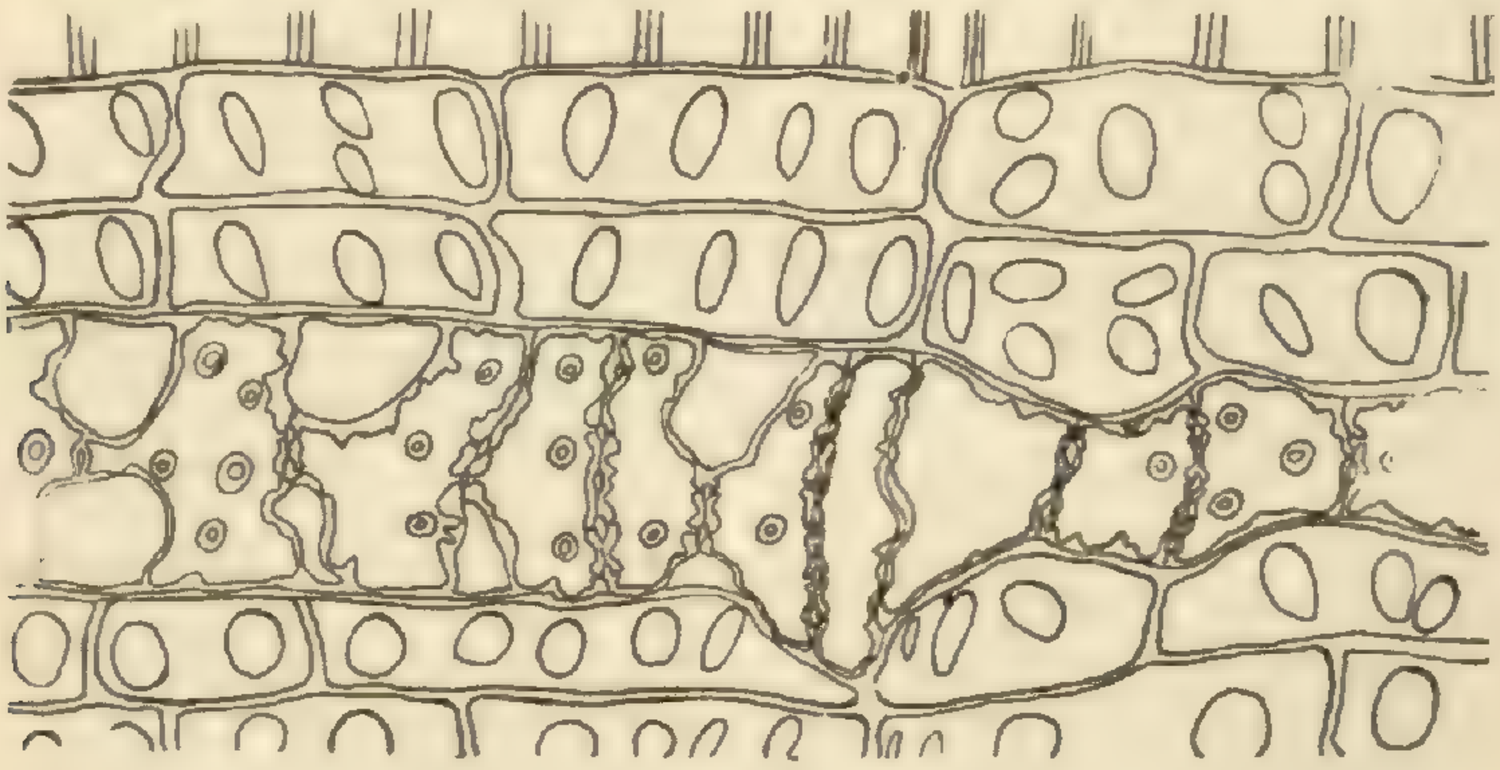

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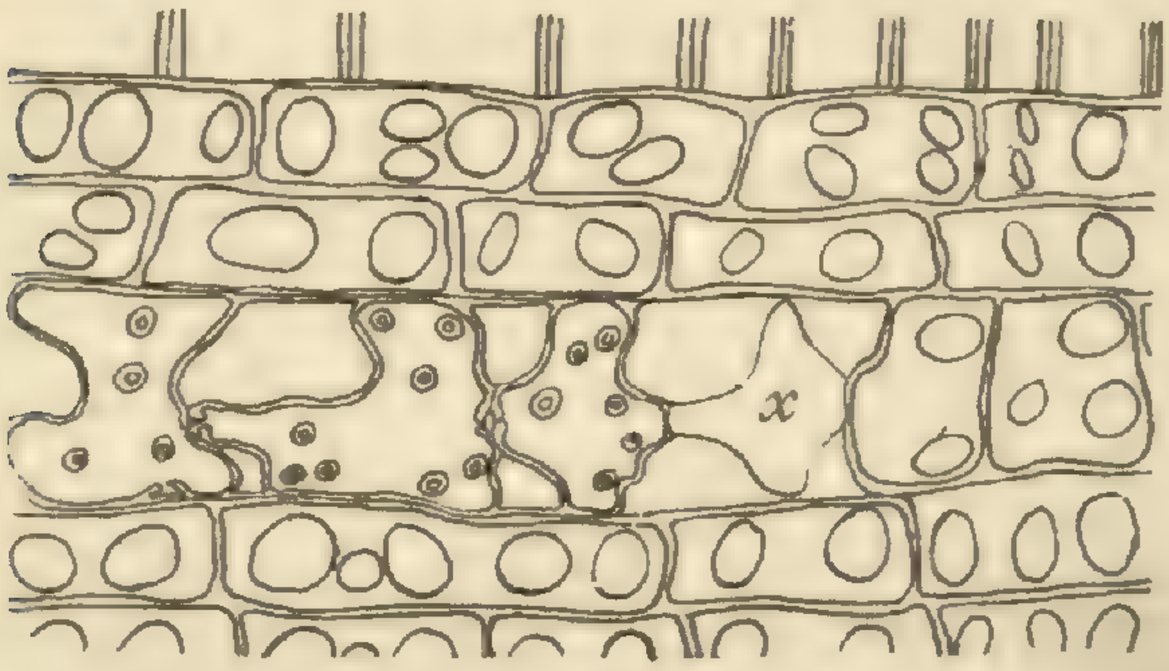
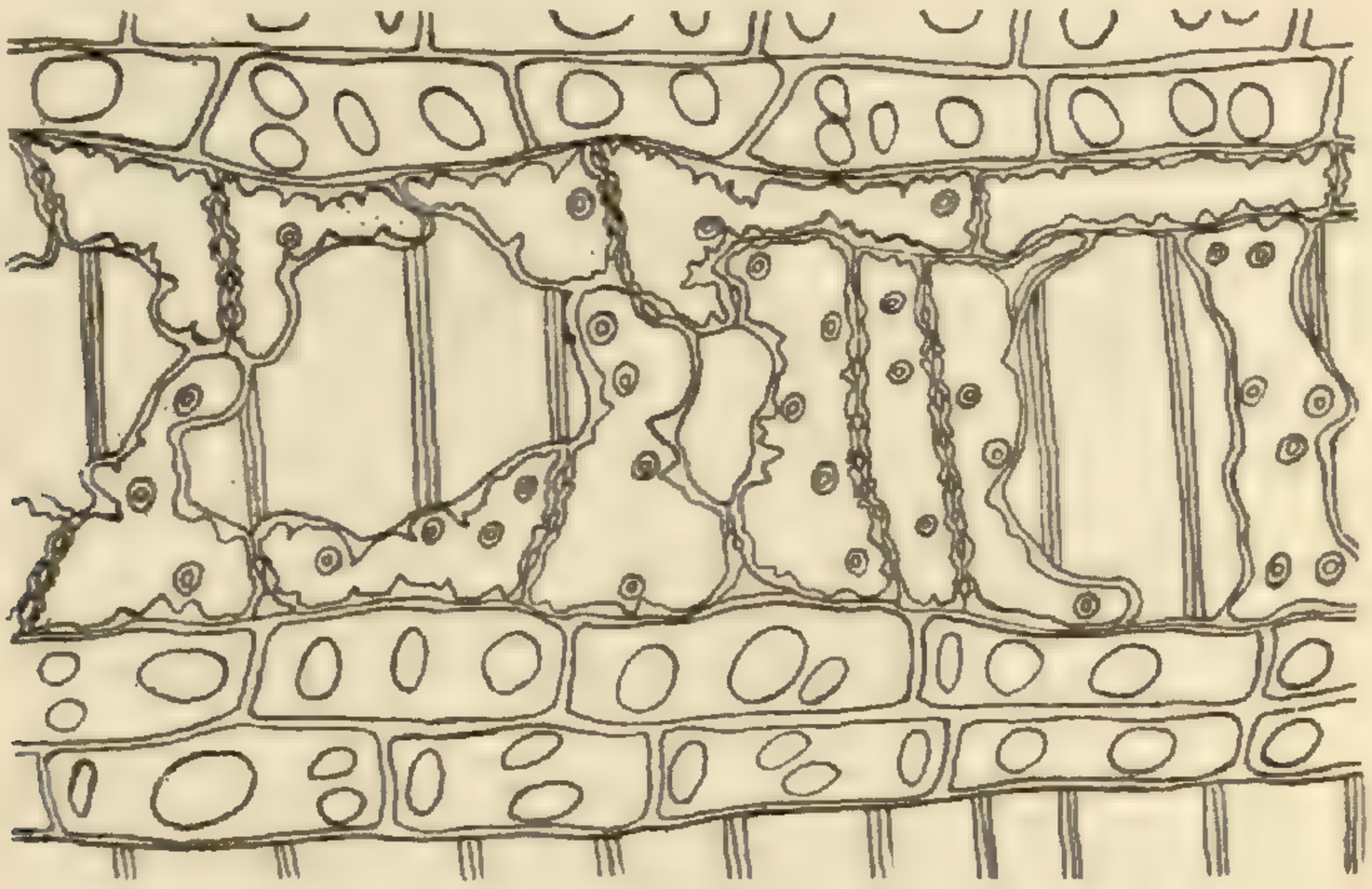


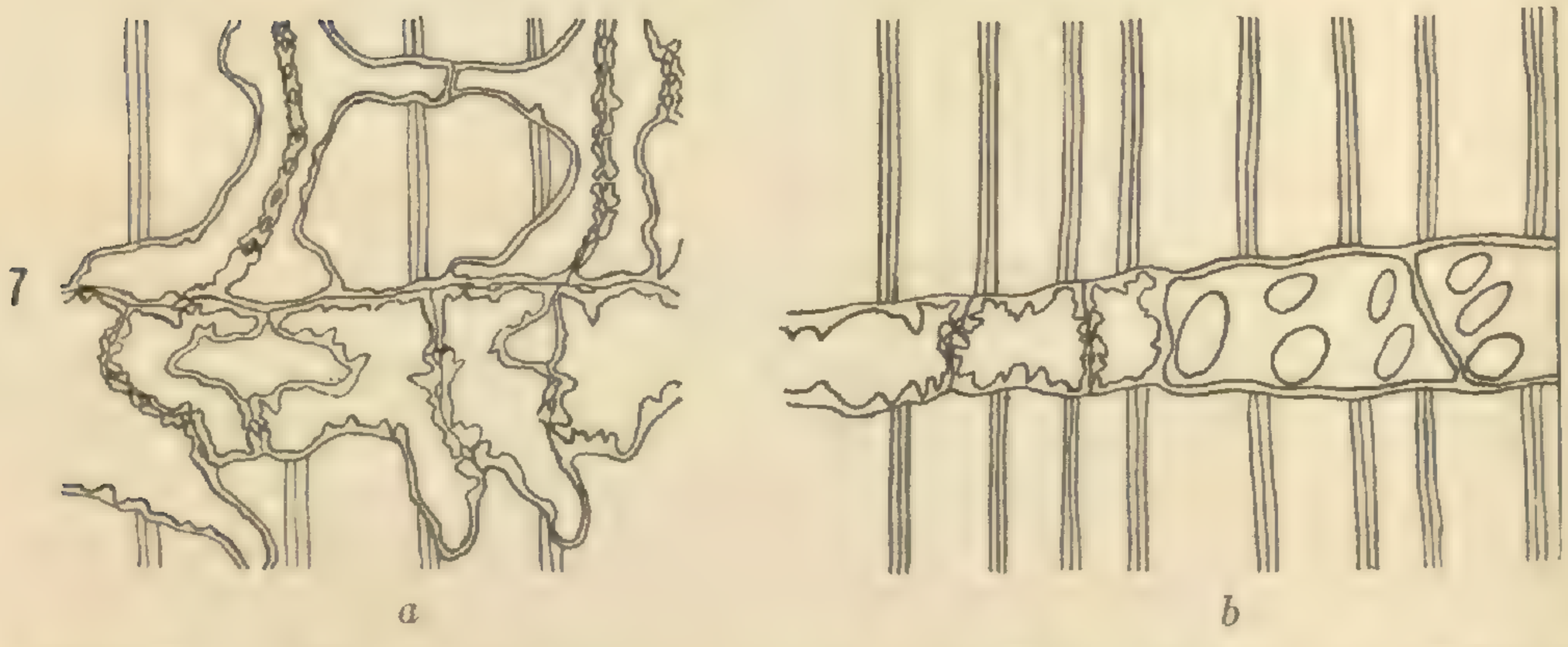
FIGS. 4, 5.—Fig. 4, *P. resinosa:* young root; the transformation of short tracheids to interspersed ray tracheids, and the fusion of rays; fig. 5, *P. Strobus:* young root; the replacement of ray tracheids by parenchyma; at *x* is a degenerating tracheid.

The approach of the rays does not always end in the production of one with interspersed tracheids. When the rays have drawn together till the intervening tracheids have formed true ray tracheids or are on the point of doing so, then these elements are often replaced by a row of parenchyma cells which soon assume the ordinary form and size. In fig. 5 at the left are the short transitional tracheids which are replaced at the right by high parenchyma cells. Farther toward the cambium these gradually become lower and indistinguishable from other cells of the ray.[1] Instances were also observed where the

[1] In this drawing, and in the others as well, with the exception of figs. 8, 9, 14–16, the simple pitting of the wall of the parenchyma has been used to distinguish this tissue from the tracheary elements with their bordered pits, the nuclear and protoplasmic contents of the former being omitted.

fusion of rays eliminated a row of tracheids without replacement by parenchyma. The tracheids were simply "pinched" out, only the parenchyma cells continuing. In a few cases, even after true marginal ray tracheids had been formed as above indicated, the rays drew together and fused, with the result that the marginal ray tracheids were "pinched" out.





FIGS. 6, 7.—Fig. 6, *P. resinosa:* young root; illustrating the formation of a double row of ray tracheids; fig. 7, *P. resinosa:* young root; formation of a wholly tracheidal ray, and its transformation into a parenchymatous one.

The origin of the marginal and interspersed ray tracheids and their relationship to the fusion of rays have been described. The more complicated case of the formation of two rows of tracheids on the margin of a ray is partly illustrated in fig. 6. At the left, toward the pith, are two rows of transitional tracheids touching end to end. Beyond the figure, nearer the medulla, these have been formed from a single row of longer tracheids. Toward the cambium the row on the

margin of the upper ray settles down to form regular ray tracheids while the other remains transitional. A repetition of the process in this row gives rise, beyond the figure, to a double series on the margin of the upper ray. In many cases, however, the second row is formed without the intervention of the transitional cells, this stage being either hurried over or completely omitted.

The only kind of ray tracheid whose formation has not yet been described is that composing the wholly tracheidal ray. When the rays are far apart, two or more divisions may take place in the long tracheids instead of the usual single one. Then one or more rows of transitional cells are formed midway between the rays, with other rows above and below, that is, touching the rays. When the latter rows separate from the central ones, these continue as irregular tracheidal cells which gradually become regular, forming a completely tracheidal ray. Fig. 7 represents only the ends of the series, a considerable space at the center being left out; in *a* are two rows of irregular tracheids, the lower of which settles down to form the completely tracheidal ray seen in *b*.

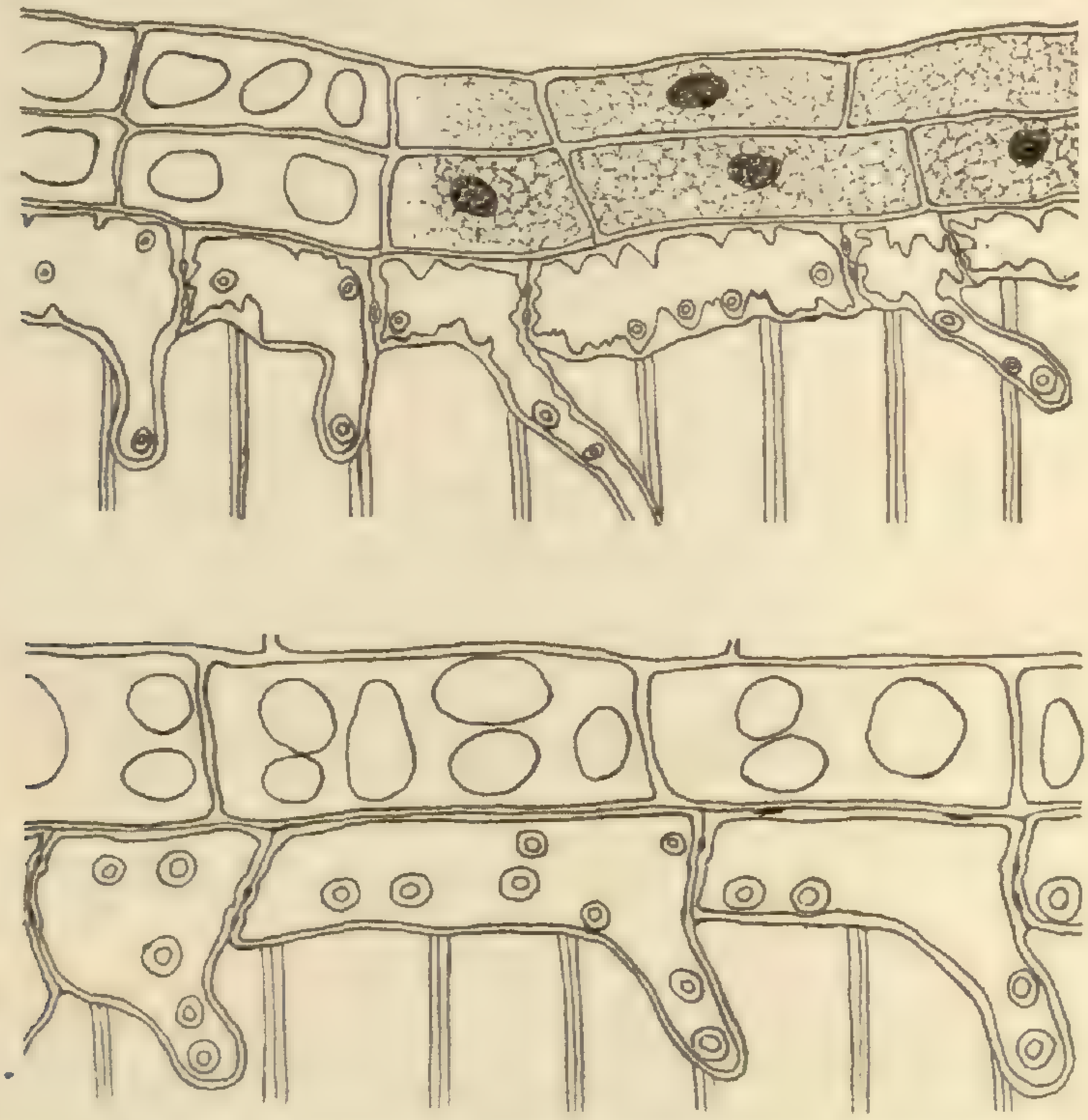
At the right in figure 7*b* another phenomenon is illustrated. This is the replacement of a tracheidal ray by a parenchymatous one. It is not an abnormality in this section, for numerous examples were seen. In fact it seems to be the common method of origin for secondary rays, that is for ones which do not run to the pith. Owing to the yearly increase in the circumference of the wood, many new parenchyma rays must be formed if the number in a given area is to remain at all constant, and it seems easier for them to be produced from cambial cells which give rise to ray tracheids than from longer ones which give rise to wood tracheids.

FIG. 8.—*P. resinosa:* young root; the development of a ray tracheid at the cambium.

In the development of some of the ray tracheids at the cambium further evidence is afforded of the origin of these structures from tracheary tissue. In fig. 8 the cambium is at the right. It has just given off a tracheid whose upper end is

"turning" along the ray and developing the buttresses characteristic of the ray tracheids of the hard pines. The lower part remains smooth. At this stage then, it is quite intermediate between a wood tracheid and a ray tracheid.

Farther from the cambium whole rows of tracheidal cells may be observed, each with a long tail-like projection extending from one



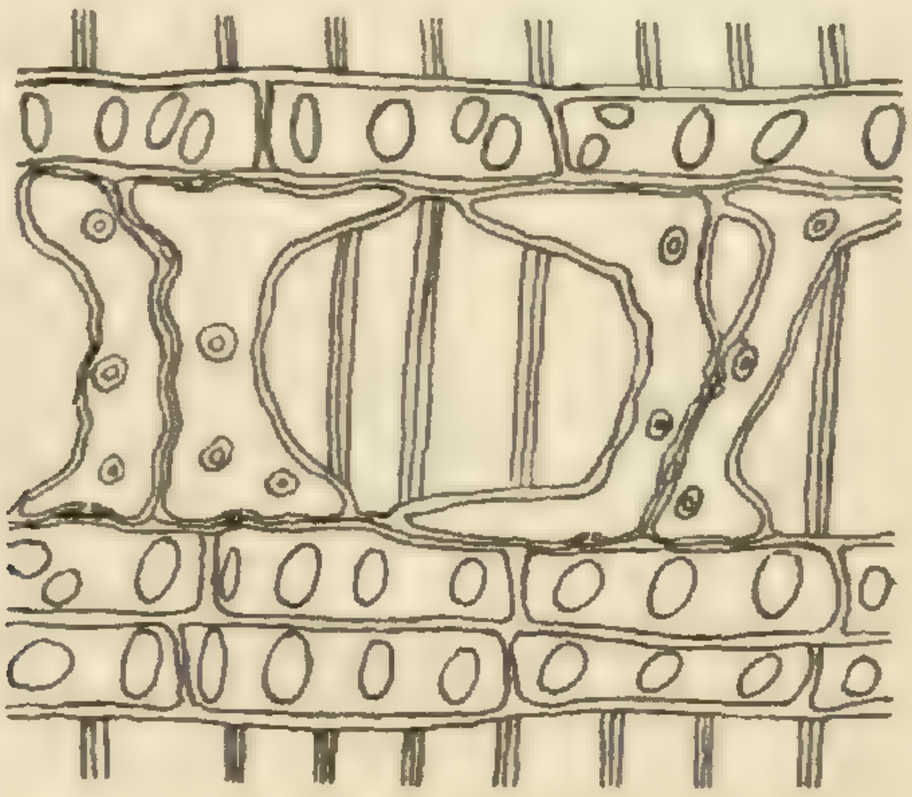
FIGS. 9, 10.—Fig. 9, *P. resinosa:* young root; a row of ray tracheids with tail-like projections; fig. 10, *P. Strobus:* adult root; ray tracheids with "tails."

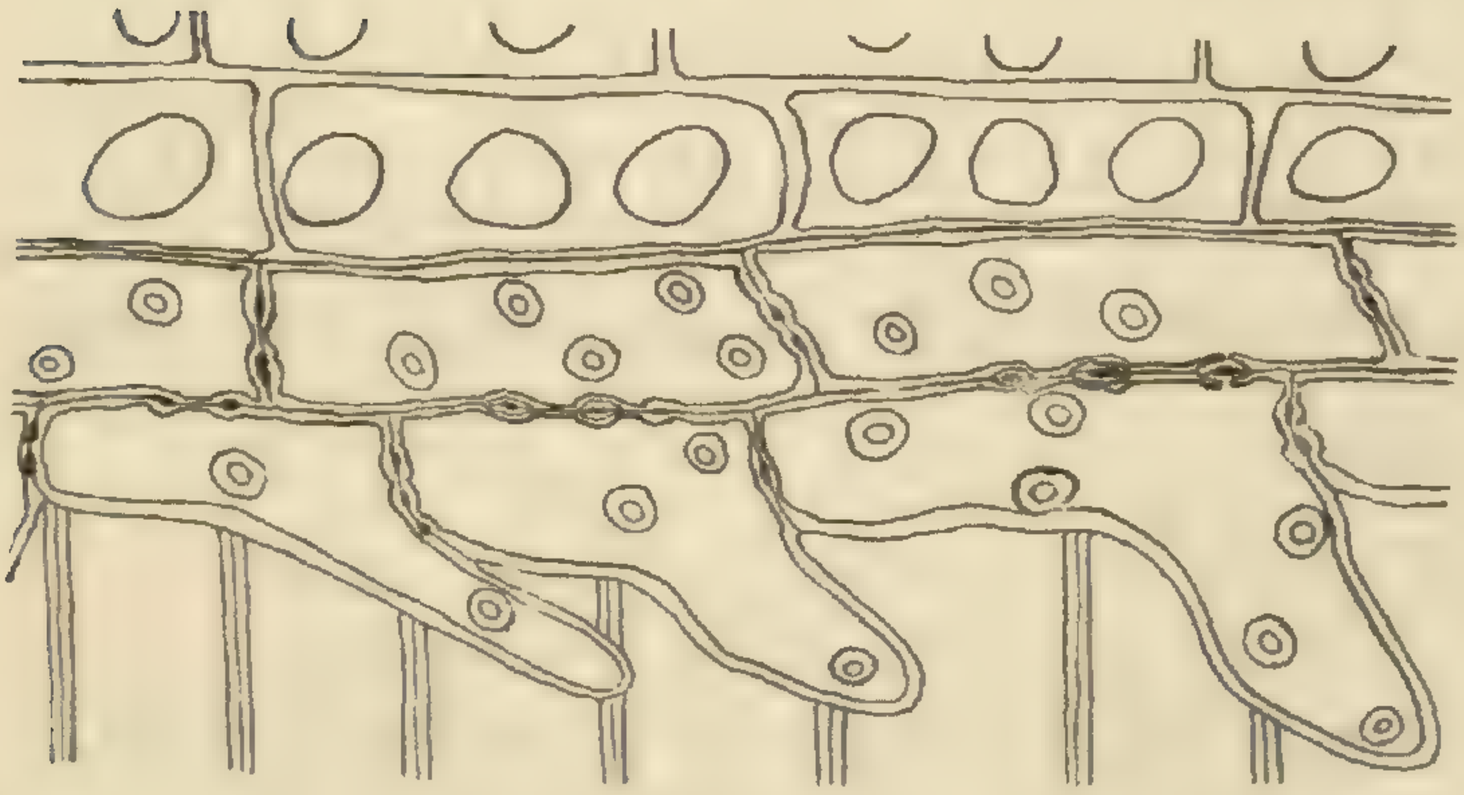
end (fig. 9), and this end is always the one nearer the cambium. The "tail" is evidently the smooth part of the tracheid as seen at the cambium. Moreover, in *Pinus resinosa* the "tail" lacks the characteristic dentations present on the rest of the cell. Apparently then it is the result of an incomplete shortening of the tracheid. Fig. 10, from an old root of *Pinus Strobus*, shows that these projections persist in the mature wood, but, as is to be expected, they are neither so numerous nor so conspicuous.

Stem

The root is admittedly more conservative than the stem. Accordingly in the latter the evolutionary processes are not so well repre-

sented. There is a hurrying over the early stages, so that an actual series can rarely be observed. Nevertheless, the transitional form of tracheid is occasionally found, and has been drawn in fig. 11 from the second year's growth of *Pinus Strobus*. Tail-like projections are quite common, and have been illustrated in fig. 12.





FIGS. 11, 12.—Fig. 11, *P. Strobus:* young stem; transitional tracheids; fig. 12 *P. Strobus*: adult stem; ray tracheids with "tails."

The only good stem series showing the transformation from tracheids to ray tracheids was observed in old stem wood of *Pinus resinosa* which had been wounded (fig. 13). The rapidly shortening series of tracheids ends at the right in true ray tracheids with buttressed walls. In this wounded material also the tail-like projections were very numerous and very large. Both features are to be accounted for as traumatic reversions similar to those described by JEFFREY for *Cunninghamia* (2), in which form though ray tracheids are not normally present they were found in connection with a wound.

Even in the normal adult ray tracheid, however, we find indications of its tracheary origin. One of these is the occurrence of tertiary

spirals. This has been described by BAILEY (5) for some species of *Pinus* as wall as for *Picea* and *Pseudotsuga*. He states: "Ray tracheids appear to follow closely the wood tracheids. Where spirals

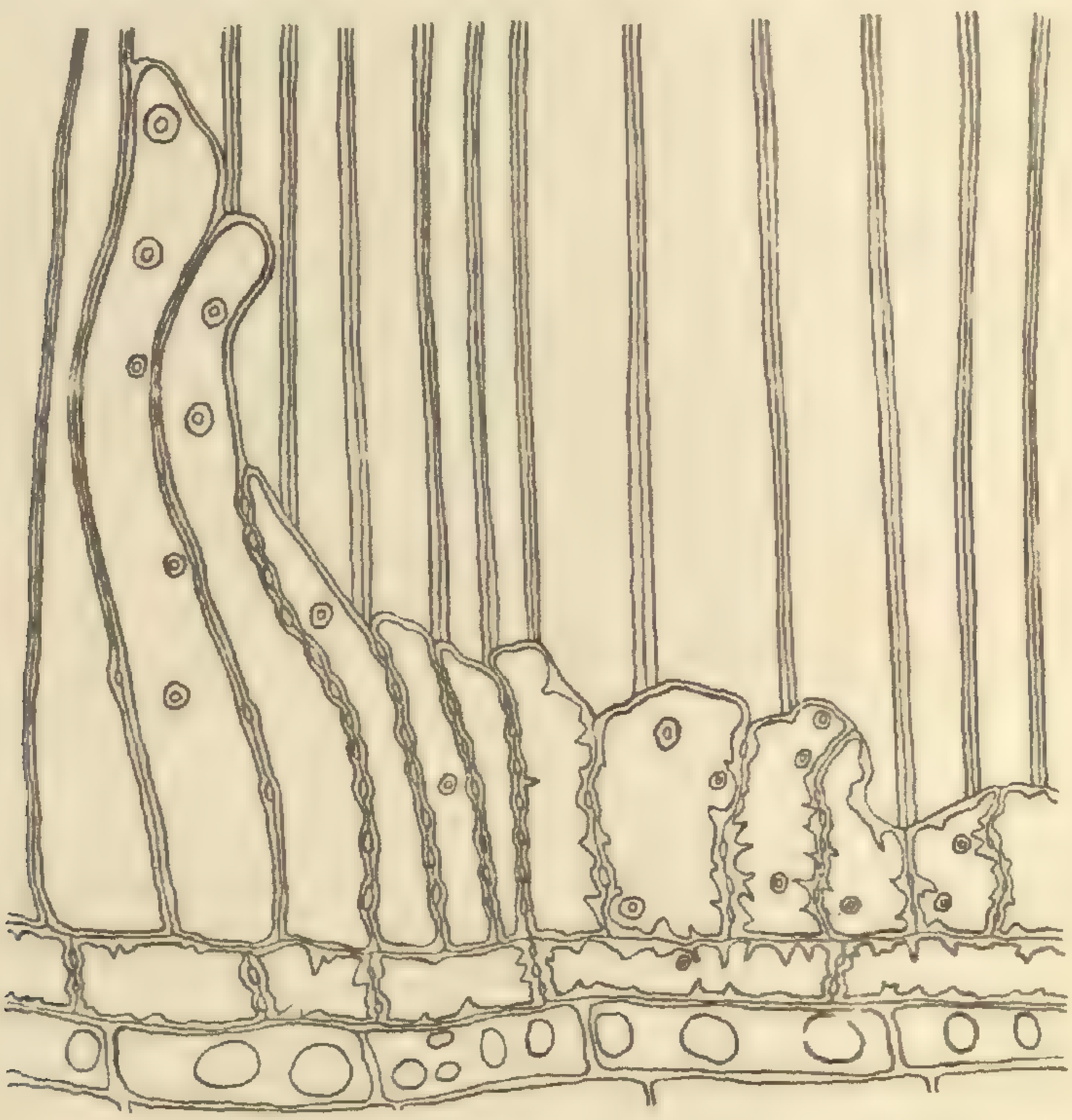


FIG. 13.—*P. resinosa:* adult stem; a series of tracheids from a wounded region, showing transformation to ray tracheids.

are strongly developed (summer wood) in the latter elements, they will also appear in the former." This concomitant occurrence of tertiary spirals on the elements in question argues community of origin.

Seedling

So far the study of the seedling has presented no features not observed in the corresponding regions of the adult, except that here the ray tracheids are later in appearing.

Cone axis

True ray tracheids are quite absent from the cone axis, as JEFFREY and CHRYSLER (6) have pointed out. I have found their place taken, however, by the bent ends of the tracheids. Fig. 14 shows a tracheid

whose end is bent along a ray for a remarkable distance. Such tracheids are very common in the cone axis, more than half the rays showing at least one in some part of their short course. Evidently they do the work of the ray tracheid, and probably represent the first step in a process of turning and shortening which, as described above, ends in the production of ray tracheids. Similar bent ends are sometimes to be found in the young stem, and are evidently to be interpreted in the same way.

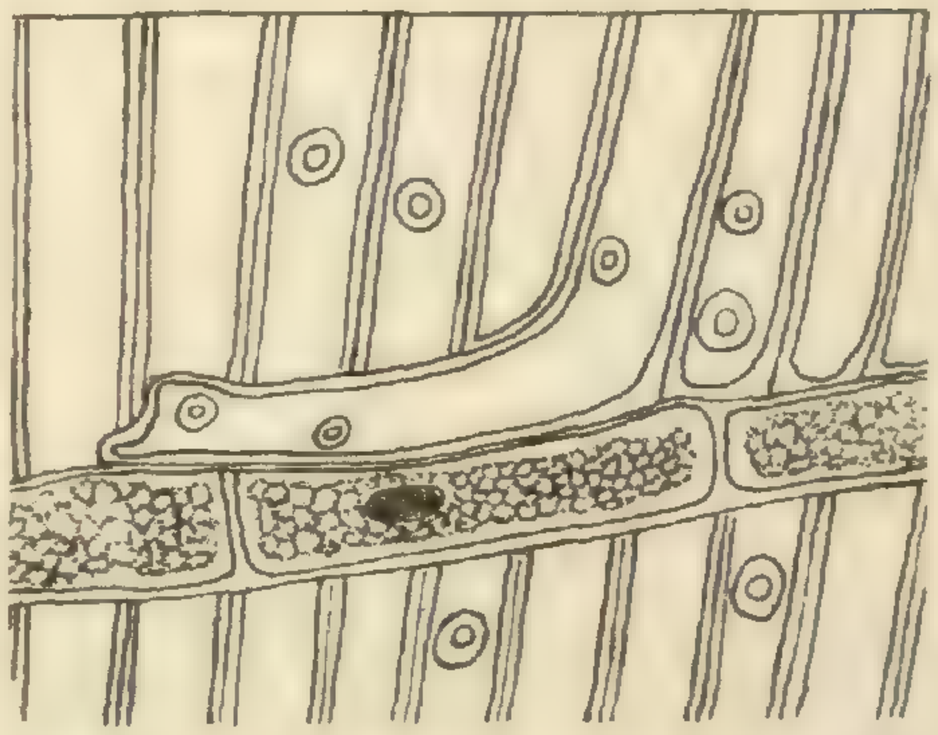


FIG. 14.—*P. Strobus:* cone axis: the end of a tracheid bent along a ray.

Relation to albuminous cells

In the light of what has been said of the origin of ray tracheids, an interesting circumstance is furnished by their relationship to the albuminous cells of the ray. STRASBURGER (7) points out the homology between the latter and sieve tubes. "The albuminous cells are higher than the ordinary cells of the ray and like sieve tubes have sieve areas, soon lose their contents, and ultimately collapse." They are then virtually *ray sieve tubes*. Now in the Abietineae, where ray tracheids are numerous, albuminous cells were always found conterminous with them through the cambial region. This is illustrated in fig. 15 even for a row of interspersed ones. In the Araucarineae and Taxaceae, where there are no ray tracheids, there are no albuminous cells. In those Taxodineae and Cupressineae where no ray tracheids were seen, no albuminous cells were found. And in *Thuja*, where ray tracheids occur sporadically, the only albuminous cells were those lining up with ray tracheids. Albuminous cells are then always associated with ray tracheids (an interesting exception is noted below). This association and their sieve tube character indicate that they bear the same relationship to ray tracheids as the sieve tubes to wood tracheids. They thus afford valuable collateral evidence of the tracheary origin of their representatives in the wood.

The exception referred to is found in *Abies balsamea*. Here almost every ray passing through the bast has albuminous cells on its margin,

but very few have ray tracheids. The albuminous cells are never in line with the parenchyma cells of the ray, but always above or below them. Often they are in line with two or three degenerating cells on the wood side. These facts support the view of JEFFREY (**2**) that the scarcity of ray tracheids in certain Abietineae, including *Abies*, is the result of degeneration. The albuminous cells, elsewhere inseparable companions of the ray tracheids, persist, while the ray tracheids themselves have disappeared. The latter are probably represented by the degenerating cells mentioned.

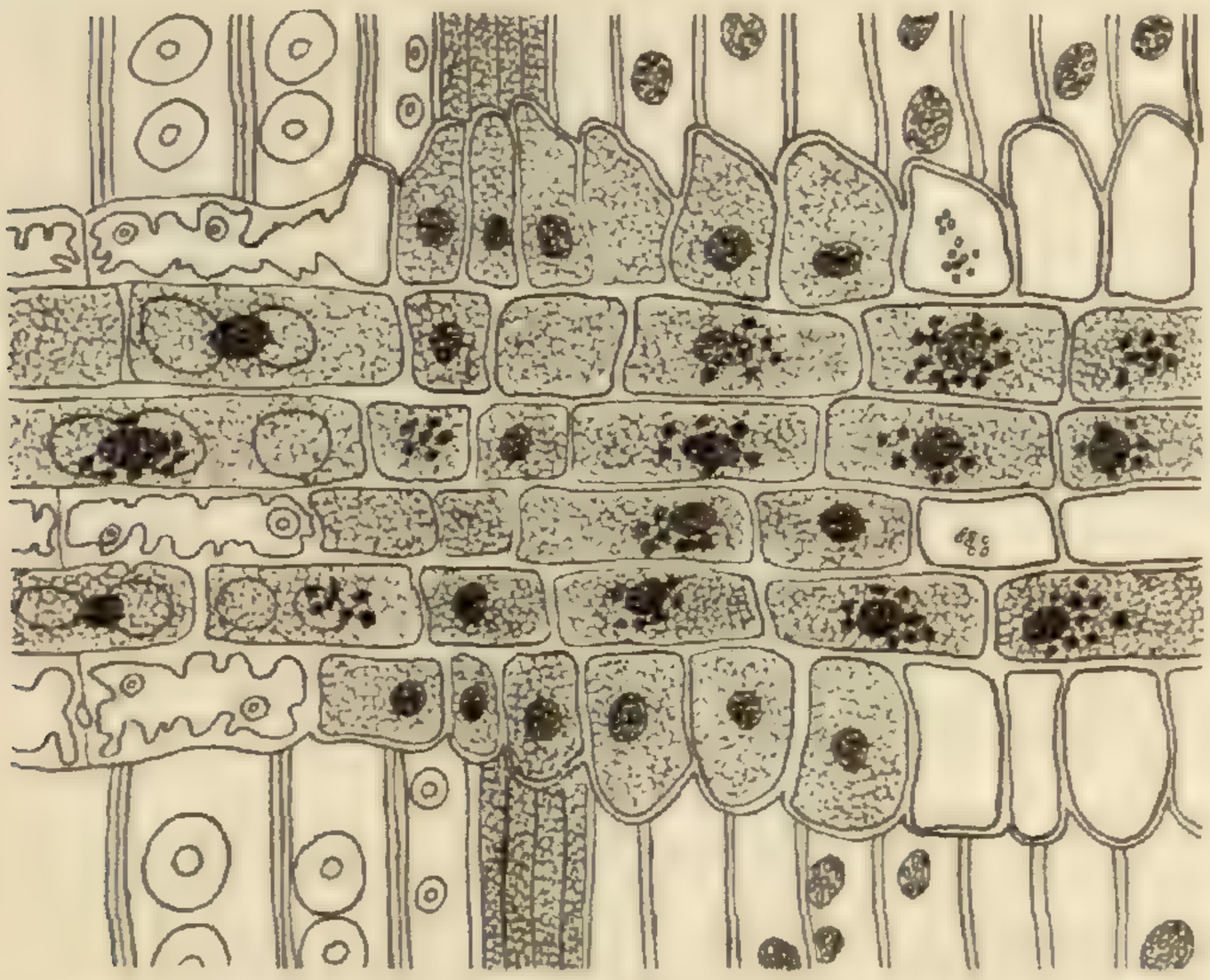


FIG. 15.—*P. resinosa:* old stem; cambial region showing albuminous cells in line with ray tracheids.

Another observation supporting this view is that of the occurrence of ray tracheids in the wounded root of *Abies amabilis*. Hitherto all observers have reported ray tracheids absent from the wood of this species. Yet in a piece of root wood which had been wounded several times, undoubted ray tracheids were developed in considerable numbers. This phenomenon parallels the traumatic revival of ray tracheids in *Cunninghamia* described by JEFFREY (**2**), and admits of a similar interpretation, in this case their ancestral presence in the genus *Abies*.

General considerations

The character and relationships of the ray tracheid have been described in the various regions of the individual plant. As has been shown, it is in the young root that the proof of its origin from tracheary tissue is most conclusive. Here transitions were observed from short tracheids extending between the rays to ray tracheids of all kinds. A significant feature, which has not yet been emphasized in connection with these transitional areas, is the occurrence of degenerating cells. One of these has been incidentally illustrated in fig. 5 at *x*. They

are structureless, shadowy outlines replacing transitional tracheids, which they resemble in form, although often somewhat more irregular. They occur in considerable numbers wherever the former elements are found, and are evidently to be regarded as "degeneration products," to which transitional structures are always subject. As such they emphasize the transitional character of the regions in question, and help to complete the chain of evidence for the origin of the ray tracheids from tracheary tissue.

PENHALLOW'S argument (1) for his theory that ray tracheids are derived by modification from the parenchymatous cells of the ray, is the occurrence of ray tracheids conterminous with parenchyma cells. But this is so rare that DEBARY (8) was led to assert that it never occurred. I must confirm PENHALLOW'S observation, however, especially in the young plant, where such an appearance is more common than in the adult. I have observed and figured this feature in the formation of secondary parenchymatous rays from wholly tracheidal ones (fig. 7), and in the replacement of interspersed ray tracheids by parenchyma (fig. 5). I have observed also a similar replacement of marginal ray tracheids by parenchyma cells. In these instances, however, it is to be noted that the parenchymatous cells are toward the cambium (to the right in the figures), and so *replace tracheary elements*, the reverse of what is required from PENHALLOW'S point of view. This is indicated in the very figure which PENHALLOW uses to illustrate the fact that ray tracheids may abut on parenchyma cells (his figure is reproduced herewith, fig. 16). The direction in which the oblique end walls are inclined, and in which the tail-like projection points, which is seen on one of the ray tracheids on the top of the ray, indicates, as shown above (figs. 8–10, 12), that the cambium is to the left of his figure. The parenchyma cell which is in line

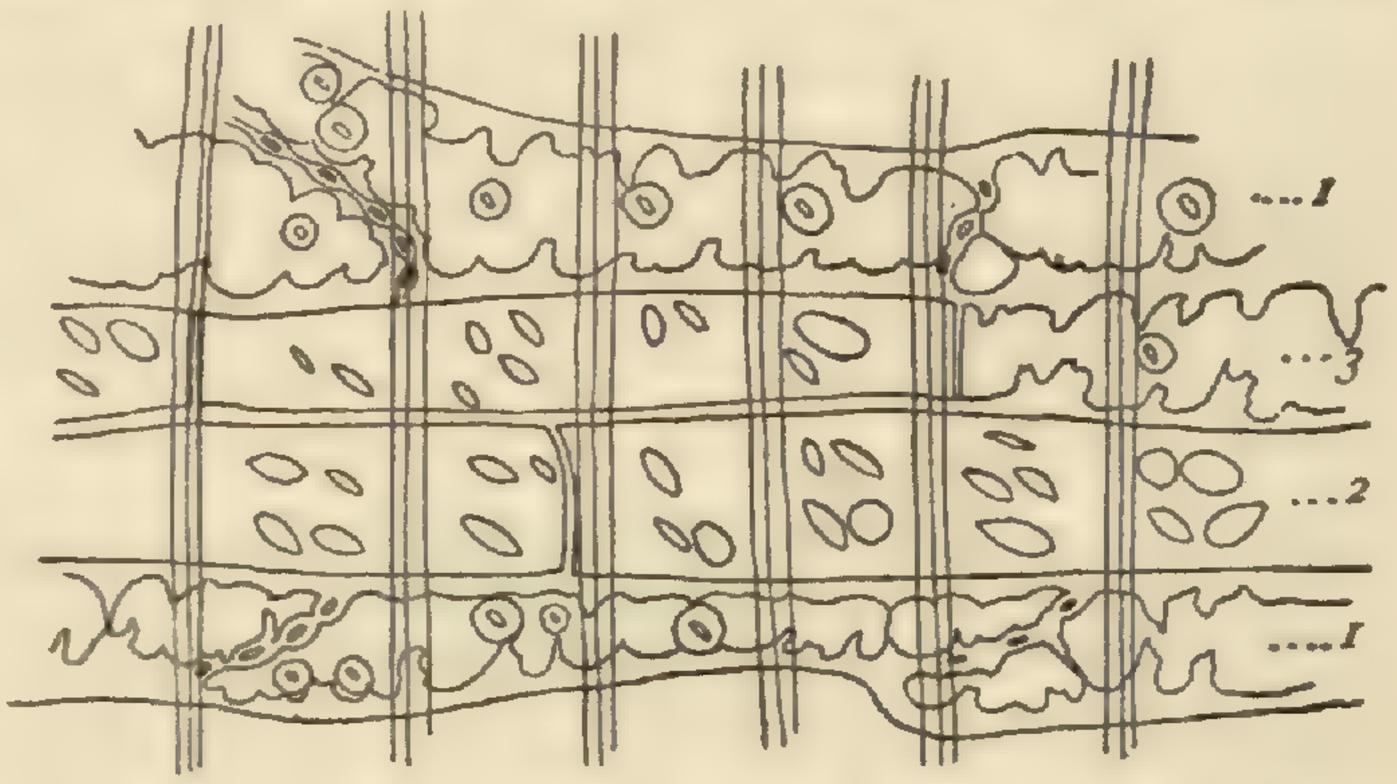


FIG. 16.—*P. serotina:* medullary ray showing (1) the ray tracheids with dentate walls, (2) the structure of the parenchyma cells, (3) tracheids conterminous with parenchyma cells.—From PENHALLOW (1).

with the ray tracheid is then nearer the cambium, and so what we really have is the replacement of a row of tracheary elements by parenchymatous ones. The origin of such a row of ray tracheids is to be looked for toward the pith, and, as I have shown above, the ray tracheids arise here either in connection with transitional tracheids, or, when these are omitted, above or below the ray and not in line with parenchyma cells.

The intimate study of the medullary ray from its beginning at the pith in the different regions of the individual plant, besides disclosing the origin of the various types of ray tracheid, has drawn attention to important features in the distribution of these structures. KNY has called attention to their absence in the first year's growth of the stem, and JEFFREY and CHRYSLER state that they are not present in the seed cone. In the young branch of *Pinus Strobus* they appear sporadically during the second and third years, and then increase slowly in number until the adult condition is attained after about ten years. In the seedling they are still later in appearing, as is also the case in the young root. In the latter region they never become so numerous as in the stem. In *Pinus resinosa* they appear in abundance much earlier and increase in number much more rapidly, reaching the adult condition in five or six years. They are never found in the cone axis of either species. Thus in the primitive regions of the plant ray tracheids do not occur, and therefore they must be regarded as specializations. That they are of cenogenetic origin is further indicated by the fact that in the older pines, the Pityoxyla of the Cretaceous, as described by JEFFREY and CHRYSLER (**6**), no ray tracheids occur.

In view of their origin and distribution, ray tracheids are regarded as specialized structures and their phylogenetic meaning so interpreted. Those woods in which they are most abundant are considered most modern, unless, as in *Abies*, it can be shown that they have been secondarily lost. Their character when present is as important as their number. For example, if the early growth shows many transitional elements or a large development of tail-like projections, then the wood is stamped as primitive. Again, the smooth-wall form in the soft pine is more tracheid-like and therefore more primitive than the dentate form of the hard pine, an inference which

is strengthened by the earlier and more rapid development of ray tracheids in *Pinus resinosa* than in *Pinus Strobus*.

Summary

1. In the young root complete transitions may be observed from short tracheids extending between the rays, to ray tracheids both marginal and interspersed. In the young stem only remnants of the transition usually remain. The complete series, however, may occur traumatically.

2. Further evidence of the origin of ray tracheids from tracheary tissue is found in (1) their development in the cambial region of the young plant, (2) the occurrence of tail-like projections, and (3) the possession of tertiary spirals.

3. The occurrence of ray tracheids bears a definite relation to that of albuminous cells.

4. In *Abies* the possession of albuminous cells and the traumatic occurrence of ray tracheids indicate that the latter are vestigial.

5. The regional and fossil distribution of ray tracheids indicates their ancestral absence in the pines.

6. The hard pines are more specialized than soft ones.

7. The large rays of *Pinus* are usually formed by the fusion of smaller ones.

8. Ray tracheids are often replaced by parenchyma cells. The importance of this in the formation of secondary parenchymatous rays has been indicated.

This study was undertaken at the suggestion of Mr. R. B. THOMSON and carried on with his constant advice. My warmest thanks are due to him for quite exceptional kindness throughout the course of the work.

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ON THE RELATIONSHIP BETWEEN THE LENGTH OF THE POD AND FERTILITY AND FECUNDITY IN CERCIS

J. Arthur Harris

(WITH ONE FIGURE)

It is well known to botanists that the egg cell is not the only structure affected by fertilization. Goebel points out[1] that in the Hepaticae an accompanying result is often seen in the production of a further development of the envelopes of the ripening sporangium. Again, in the same work he suggests[2] that the stimulus exercised by pollination in the flowering plants is most probably chemical. The preparation of the ovules for fertilization is dependent in some cases upon pollination. For instance, in such plants as *Corylus*, *Alnus*, *Quercus*, and some of their allies, there is no sign of the placenta in the ovary, to say nothing of ovules, at the time of pollination. In most species of Orchidaceae the ovules are laid down at the time of pollination, but still are rudimentary. The stimulus exercised by the pollen tube induces the further development of the female sexual apparatus in these plants.

Pfeffer[3] joins with Goebel in considering that the penetration of the pollen tube may serve as a stimulus to the development of the ovary, and cites the seedless fruits studied by Müller-Thurgau and the observations on *Ficus* by Treub.

Jost[4] writes: "The germination of the pollen tube has an exciting influence on the development of the fruit. This is particularly noticeable in certain cultivated plants, which, as for example currants and sultana raisins, produce no seeds, the ovules having degenerated. If the stigmas of these plants be not pollinated, the fruit fails to develop, but pollination leads to development without leading to any fertilization."

[1] Organography of plants **2**:105. 1902.

[2] *Op. cit.* **1**:269–270. 1900.

[3] Physiology of plants (English transl.) **2**:173. 1900–1906.

[4] Lectures on plant physiology (English transl.) p. 370. 1907.

This is not the place for a review of the literature bearing upon these interesting chemical, physiological, and morphogenetic problems, however one wishes to designate them. The views of the three botanists just cited are sufficient to show the interest which is being taken in these problems. Several writers have contributed to the literature. Without any attempt at arrangement for priority or extent of investigation, I mention EWART (**1, 2**), SOLACOLU (**7**), TREUB (**8**), MÜLLER-THURGAU (**5**), NOLL (**6**), and FITTING (**3**). FITTING (**4**) has recently given a review, with a bibliography, of the chief literature in connection with an account of his own work on the Orchidaceae. From his experimental studies in this family he is led to the conclusion that the stimuli involved in the ontogeny of the fruit are in part due to an organic substance, not an enzyme, external to the pollen grain, in part to the growth of the pollen tubes, and finally in part to the development of the fertilized ovules.

The observations of the authors mentioned above deal chiefly with the influence of pollination as a stimulus inducing the development of the ovary up to a stage where the fertilization of the ovules is possible, or a little beyond. These phases of the problem are much more easily studied experimentally than that of the influence of the developing ovule upon the growth of the ovary. The present investigation bears upon this point.

If the developing seed excretes some substance which acts as a stimulus to the development of the ovary wall, or in some other manner exerts an influence upon it, it seems not unreasonable to suppose that the effect would be greater if several seeds were developing than if there were only one or a very few.

Our problem is essentially this: Does the number of ovules which develop to matured seeds influence the size of the fruit, and to what extent?

In all of the pods which have matured at least one seed, the stimulus to development due solely to the penetration of the pollen tube (as distinguished from the possible influence of the developing zygote) should be the same for all pods, unless the quantity of pollen tubes which penetrate the tissue of the style differs from ovary to ovary, and the intensity of the stimulus is to some extent proportional to their number. The problem is surrounded by a good many difficul-

ties. There seem to be at least four ways in which a relationship between the number of seeds developing and the size of the fruit might arise.

a. Fruits with a larger number of ovules are apt to be larger, if for no other reason, simply because the placental space required is greater. In the long run fruits with larger numbers of ovules also have larger numbers of seeds,[5] and an influence on fruit length at first attributed directly to the development of the seeds might be due indirectly to the number of ovules.

b. The space required for the matured seeds might, through the purely mechanical effects of crowding, result in the fruits with greater numbers of seeds being larger in size.

c. The developing seed might by means of some excreted product, or in some manner not yet suggested, directly induce a greater development of the ovary.

d. Both the number of ovules developing into seeds and the size attained by the fruit may be to some measure dependent upon some other character; say, for example, the position of the fruit on the inflorescence axis, or the number of fruits developing per inflorescence. The correlation between them might then be due merely to their mutual dependence upon some other character.

In the literature one finds only a few references to the relationship between the fertility of a fruit and its size. EWART (1) gives tables showing numbers of seeds and mean weight of fruit for three series of 125, 48, and 134 fruits of one variety of apples, which indicate that weight increases with number of seeds. According to EWART, MÜLLER-THURGAU found that in apples and pears the size of the fruit and the number of seeds are interdependent. MÜLLER-THURGAU cut off four of the five stigmas in the pear blossom, fertilized the remaining one, and thus produced asymmetrical fruit. EWART concludes: "Es steht demnach ohne zweifel fest, dass den Kern einen Wachtumsreiz auf die zur Fruchtbildung bestimmten Gewebe ausübt."

In view of the four possibilities suggested above, I think it is quite evident that great caution should be used in asserting that the number of ovules developing into seeds has *per se* any influence upon

[5] This statement is based on the results of many series of unpublished observations.

the size of the fruit. I believe that in such cases the analytical methods of modern higher statistics applied to large bodies of data are fitted to give results of real value.

The purpose of the present paper is to present the results of an attempt to measure the intensity of the interrelationship between the length of the pod and (*a*) the number of ovules formed, (*b*) the number of seeds developing, and (*c*) the fecundity, that is, the ratio of number of seeds developing to number of ovules formed per pod, in *Cercis canadensis*.

As material for a first study, the number of ovules formed and the number of seeds developing per pod were counted and the length measured in 3,000 pods, collected at Meramec Highlands, St. Louis, Missouri, in the autumn of 1905. To secure as representative material as possible, 50 pods from each of 60 individuals were taken. The measurements of pod length were taken to the nearest millimeter, and then grouped in classes of three millimeter range for purposes of calculation.

TABLE I

FERTILITY AND LENGTH OF POD FOR 3,000 *Cercis* FRUITS

	45–47	48–50	51–53	54–56	57–59	60–62	63–65	66–68	69–71	72–74	75–77	78–80	81–83	84–86	87–89	90–92	93–95	96–98	99–101	102–104	
1	. .	. .	. .	1	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	1
21	. .	. .	1	2	1	7	4	4	1	. .	. .	. .	. .	1	. .	. .	. .	. .	. .	. .	21
13	2	1	1	3	3	2	. .	1	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	13
49	1	1	1	3	6	8	9	8	3	5	2	1	1	. .	. .	. .	. .	. .	. .	. .	49
120	. .	. .	1	1	8	10	20	24	27	18	14	4	1	1	. .	. .	. .	. .	. .	. .	120
4	. .	. .	. .	. .	1	1	2	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	4
101	. .	. .	. .	3	9	14	22	16	12	11	7	4	2	1	. .	. .	. .	. .	. .	. .	101
309	. .	. .	2	11	9	37	72	62	56	57	57	24	8	4	. .	. .	. .	. .	. .	. .	309
569	1	. .	. .	2	4	23	48	78	94	102	99	60	40	13	5	. .	. .	. .	. .	. .	569
1	. .	. .	. .	. .	. .	. .	1	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	1
10	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	10
138	. .	. .	1	. .	1	5	2	1	2	1	1	2	2	1	. .	. .	. .	. .	. .	. .	138
420	. .	. .	1	2	3	14	18	21	20	16	22	10	7	2	. .	1	. .	1	. .	. .	420
577	. .	. .	1	1	3	13	22	54	67	70	74	48	33	19	3	8	1	2	1	. .	577
3	. .	. .	. .	. .	2	5	17	30	58	115	115	96	59	48	20	11	. .	. .	1	. .	3
18	. .	. .	. .	1	. .	. .	. .	. .	. .	1	. .	1	. .	. .	. .	. .	. .	. .	. .	. .	18
83	. .	. .	. .	. .	. .	1	3	3	2	4	2	2	. .	. .	. .	. .	. .	. .	1	. .	83
185	. .	. .	. .	. .	1	2	7	4	10	22	16	10	6	2	1	2	. .	. .	. .	. .	185
224	. .	. .	. .	. .	. .	4	3	6	16	23	36	39	29	16	5	6	. .	1	. .	1	224
1	. .	. .	. .	. .	. .	. .	4	3	19	22	38	45	38	25	10	7	4	3	4	2	1
0	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	1	. .	. .	. .	. .	. .	. .	. .	. .	0
8	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	8
17	. .	. .	. .	. .	. .	1	. .	. .	1	1	1	3	1	. .	. .	. .	. .	. .	. .	. .	17
20	. .	. .	. .	. .	. .	. .	. .	1	. .	1	1	3	2	2	3	2	2	. .	. .	. .	20
	1	. .	. .	. .	. .	. .	. .	. .	. .	2	5	. .	5	3	1	1	2	1	. .	. .	
3000	1	4	2	9	30	51	147	255	315	391	474	487	357	232	137	47	39	6	7	7	3

Table I gives the data. In the first column to the left the number of ovules formed and the number of seeds developing per pod are

shown in the form of fractions, in which the number of ovules is given as the denominator and the number of seeds developing as the numerator. For each of the twenty-four seed-ovule classes found in our material, the frequencies of the different pod lengths are tabulated out.

The physical constants describing these characters are:

Average ovules	4.6947±0.0111
Standard deviation of ovules	0.9041±0.0079
Coefficient of variation of ovules	19.258
Average seeds	4.0613±0.0134
Standard deviation of seeds	1.0849±0.0094
Coefficient of variation of seeds	26.712
Average length of pod	76.181±0.095
Standard deviation of length of pod[6]	7.6814±0.0669
Coefficient of variation of length of pod	10.496
Average index, seeds/ovules	0.8650±0.0020
Standard deviation of index	0.1587±0.0014

These constants require no discussion here; they enable us to pass to the determination of the degree of interdependence of the fertility characters and the length of the fruit.

Consider first the correlation between number of ovules per pod and the length of the pod. We find $r_{ol}=0.4278\pm0.0101$. Remembering that correlation is measured on a scale of 0 to ±1, we see (*a*) that the sign of the relationship is positive, that is, that as the number of ovules per pod increases the length also increases, and (*b*) that the relationship is a moderately close one.

The degree of interdependence between the two characters may be made clearer by expressing it in terms of regression instead of correlation. The equation to the regression straight line is

$$y=56.119+3.634x.$$

In this case y=length of pod and x=number of ovules per pod. From this equation we see that a pod having an ovule more than the average of the population would be 3.6 mm. longer than the average length.

[6] SHEPPARD'S correction was applied to the second moment in the calculation of the constants for length of pod. It was not used for the fertility characters, where we are dealing with integral variates, nor in the seed-ovule indices.

The regression line and the empirical mean length for the different numbers of ovules per pod are shown in a diagram (fig. 1). To the eye the agreement is very good, except at the upper extreme, where the observations are relatively few. We may obtain some idea of

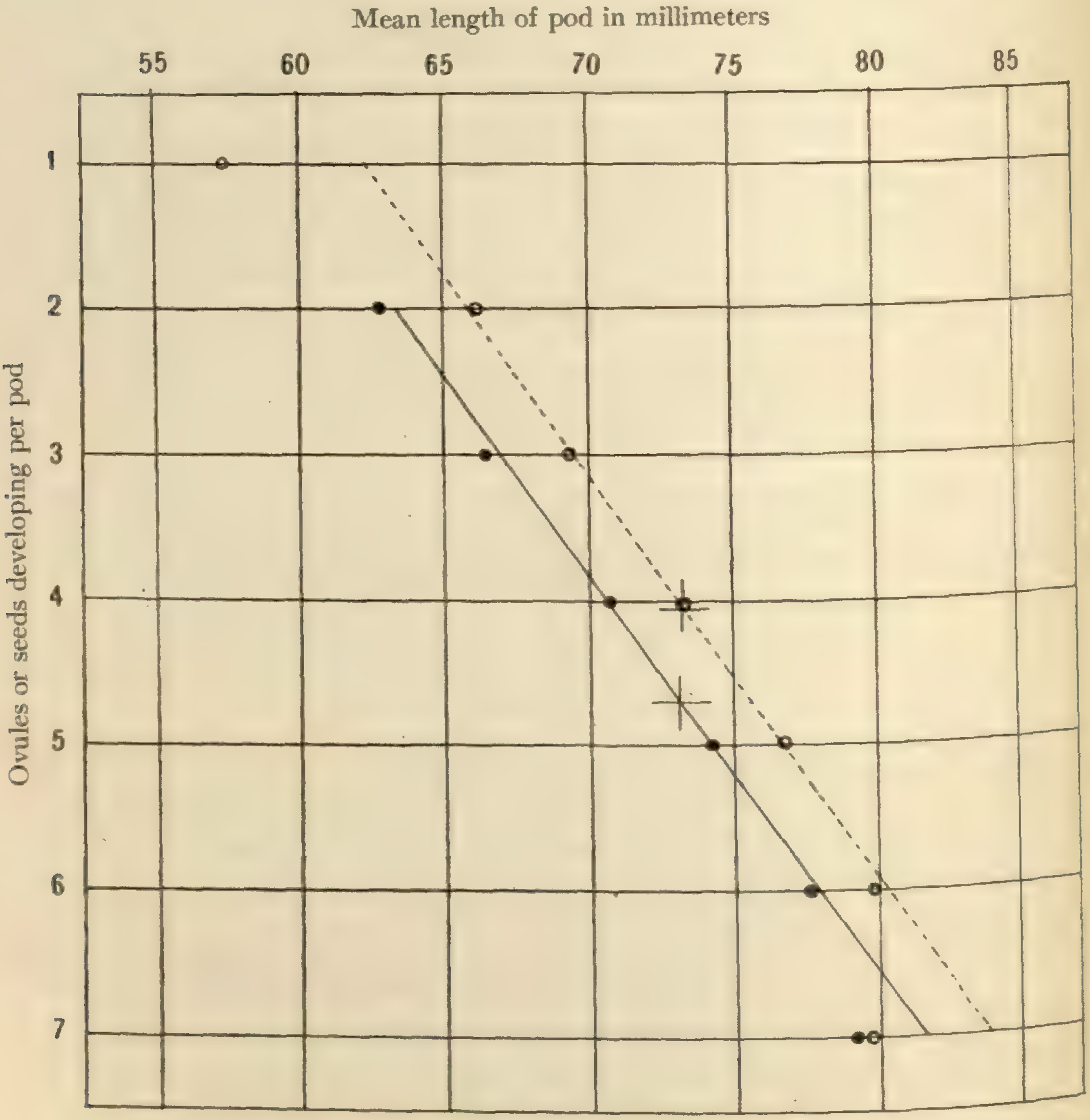

FIG. 1.—Diagram of slope of regression: straight lines, length on ovules and on seeds; solid line, theoretical length of pod for ovules; dotted line, theoretical length of pod for seeds; solid dots, observed length for ovules; circles, observed average length for seeds.

the amount of discrepancy between the theoretical line and empirical means by taking the average deviation on both sides of the line given by the equation. Considering the weight to be attached to a deviation to be proportional to the number of observations on which it is based,

we find average deviation = 0.248 mm. A discrepancy of a fourth of a millimeter in a character such as the pod length of *Cercis* may seem to most biologists quite negligible, but I rather suspect that the falling off in mean pod length in pods with seven ovules is significant. The point is of little practical importance for our present discussion.

For number of seeds maturing per pod and length of pod we find the interdependence $r_{sl} = 0.5055 \pm 0.0092$, and the equation to the regression straight line

$$y = 58.645 + 3.579x,$$

where the significance of y is as above, and x = seeds per pod. The diagram (fig. 1) shows the agreement between the line given by the equation and the empirical means. Throughout the central region of the distribution of the number of seeds developing, the fit is very good, but at both ends the observed means fall considerably below those to be expected from the equation. If these deviations are biologically significant, and not due merely to the small number of observations which fall at the extremes of the range, they indicate that both the pods developing only a single seed and those developing the maximum number of seeds are somewhat dwarfed in length as compared with the whole series of 3,000 pods. I am not yet ready to discuss the reasons for this condition.

Comparing the constant for ovules and length, and seeds and length, we find

For ovules and length, $r = 0.4278 \pm 0.0101$
For seeds and length, $r = 0.5055 \pm 0.0092$

Difference = 0.0777

Since the correlation is actually, though only slightly, higher for seeds developing than it is for number of ovules formed, it would appear that the number of seeds developing must have some connection with the length of the pod independent of the interdependence for length and ovules.

As pointed out early in this paper, one of the difficulties in asserting that there is a real physiological relationship between the number of seeds developing and the size of the fruit arises from the fact that

the correlation between the number of ovules formed and the size of the fruit may be of such a magnitude that it is impossible to tell without relatively refined statistical analysis whether the influence apparently due directly to the seeds may not be referred to the ovules. In the present case, for instance, the correlation for number of seeds developing exceeds only very slightly that for number of ovules formed.

We may determine whether the number of seeds developing has *per se* any correlation with the length of the pod by the following simple process. We sort our material into classes according to the number of ovules per pod, and then into subgroups according to the number of seeds developing, and determine the mean pod length for each of these subgroups. If now the length of the pod and the number of seeds developing are in some measure interdependent, we should expect to find significantly different mean lengths for pods of the same number of ovules, but different numbers of matured seeds.

TABLE II

MEAN LENGTH OF PODS FOR DIFFERENT NUMBERS OF SEEDS PER POD IN THE FOUR CHIEF OVULE CLASSES

NUMBER OF SEEDS PER POD	NUMBER OF OVULES PER POD			
	3	4	5	6
1.....	55.46	61.75	64.00	.....
2.....	64.24	66.94	68.73	69.00
3.....	68.37	69.06	70.37	72.00
4.....	.....	72.41	73.85	73.97
5.....	.....	.....	76.39	77.72
6.....	.....	.....	.....	79.76

Such an arrangement of the data is given in table II for the classes in which the number of observations is sufficiently large to give smooth results. Here the results are very clearly favorable to the hypothesis of a relationship between the number of seeds developing and the length of the pod, independent of the relationship for number of ovules, for the mean increases as the number of seeds increases when we work with constant numbers of ovules per pod.

The same problem may be approached in another manner, that has the advantage of giving a terse quantitative statement of the independent relationship between the number of seeds developing

and the length of the pod. The partial correlation coefficient gives the correlation between two characters, say seeds (s) and length (l) for constant values of a third character, number of ovules (o).

A necessary preliminary is to determine the correlation between number of ovules per pod and number of seeds developing per pod. We find $r_{os}=0.7297\pm0.0058$. Clearly with such a large value for the correlation between ovules and seeds we would expect some relationship between the number of seeds developing and the length of the pod, having no direct physiological significance whatever, but due merely to the fact that since number of ovules and number of seeds are closely correlated, and number of ovules and length of pod are correlated, number of seeds and length of pod *must also be correlated*. It is the influence of the ovules which we wish to remove by means of the partial correlation coefficient. The familiar formula is

$$\rho_{sl}=\frac{r_{sl}-r_{os}r_{ol}}{\sqrt{1-r_{os}^2}\sqrt{1-r_{ol}^2}},$$

which gives

$$\rho_{sl}=0.3128\pm0.0111.^{7}$$

I think this is a rather significant result. It not only shows that there is a physiological or morphogenetic relationship between the number of seeds developing and the length of the fruit independent of the correlation for ovules and length, but tells us the intensity of the interdependence as well.

There is still another way in which the influence of the ovules may be, to some extent at least, cleared away. Instead of correlating between the actual number of seeds maturing per pod and the length of the pod, the correlation between the relative number of seeds developing per pod (that is, the ratio or index seeds/ovules per pod) and the length of the pod may be found: $r_{il}=0.2906\pm0.0113$. This constant indicates very clearly that there is a real interdependence of number of seeds developing and fruit length, which is independent of the correlation for number of ovules and length of fruit.

[7] The probable error of ρ_{sl} is from the formula $E\rho_{sl}=0.67449\cdot1-\rho_{sl}/\sqrt{n}$. Mr. DAVID HERON, of University College, London, tells me that he has recently demonstrated the correctness of this formula and has the proof in press.

Comparing the two methods of obtaining the independent correlation between number of seeds and length we have:

Correlation of index and length	0.2906 ± 0.0113
Partial correlation coefficient	0.3128 ± 0.0111
Difference	0.0222

This difference is certainly of no practical importance.

Summary

1. In considering the influence of the number of seeds developing upon the dimensions attained by the fruit, the number of ovules formed cannot be disregarded, since a correlation attributed directly to the influence of the development of the seeds may be in part at least due to an interdependence between the number of ovules formed and the dimensions of the fruit. The influence of the number of ovules can be neglected only when the coefficient of correlation between number of ovules and size of fruit is demonstrated to be zero. This point is well illustrated by a series of 3,000 pods of *Cercis*, where the correlations for ovules and length is $r_{ol}=0.428 \pm 0.010$; while the correlation for seeds per pod and length is only $r_{sl}=0.506 \pm 0.009$.

2. Two methods for freeing the correlation between the number of seeds developing and the length of the fruit from the influence of the relationship between the number of ovules formed and the length of the pod are suggested; the first is the determination of the partial correlation coefficient, that is, the correlation between number of seeds and length for constant values of numbers of ovules per pod: the second is the determination of the correlation between the index $\frac{\text{Seeds developing per pod}}{\text{Ovules formed per pod}}$ and the length of the pod.

The results from the data in hand are in close agreement,

$$\rho_{sl}=0.313 \pm 0.011$$
$$r_{il}=0.291 \pm 0.011$$
$$\rho_{sl}-r_{il}=0.022$$

and we conclude that of the gross correlation of about $\rho=0.500$ for number of seeds and length of pod a considerable portion, say $\rho=0.300$ roughly, is due to some morphogenetic or physiological relationship between the number of seeds developing and the length of the pod.

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DEVELOPMENT OF THE OVULATE STROBILUS AND YOUNG OVULE OF ZAMIA FLORIDANA

FRANCES GRACE SMITH

(WITH TWENTY-TWO FIGURES)

The results of a study of the development of the staminate strobilus and microsporangia of *Zamia* were published by the writer in 1907 (1). Some of the material, sent from Miami, Florida, in June of the years 1905 and 1906 for this investigation, included ovulate cones. Later in the year 1906 an effort was made to secure a complete series of young ovulate cones, for *Zamia*, alone of the cycads of North America, exists in such profusion that whole plants may be sacrificed to secure a single small cone from each. There are some stages not yet covered by the series of cones which has been obtained, but it seems worth while at this point in the study of the material to sum up the results, and to postpone conclusions from these results and their theoretical bearing upon other cycad studies until a complete series has been gathered.

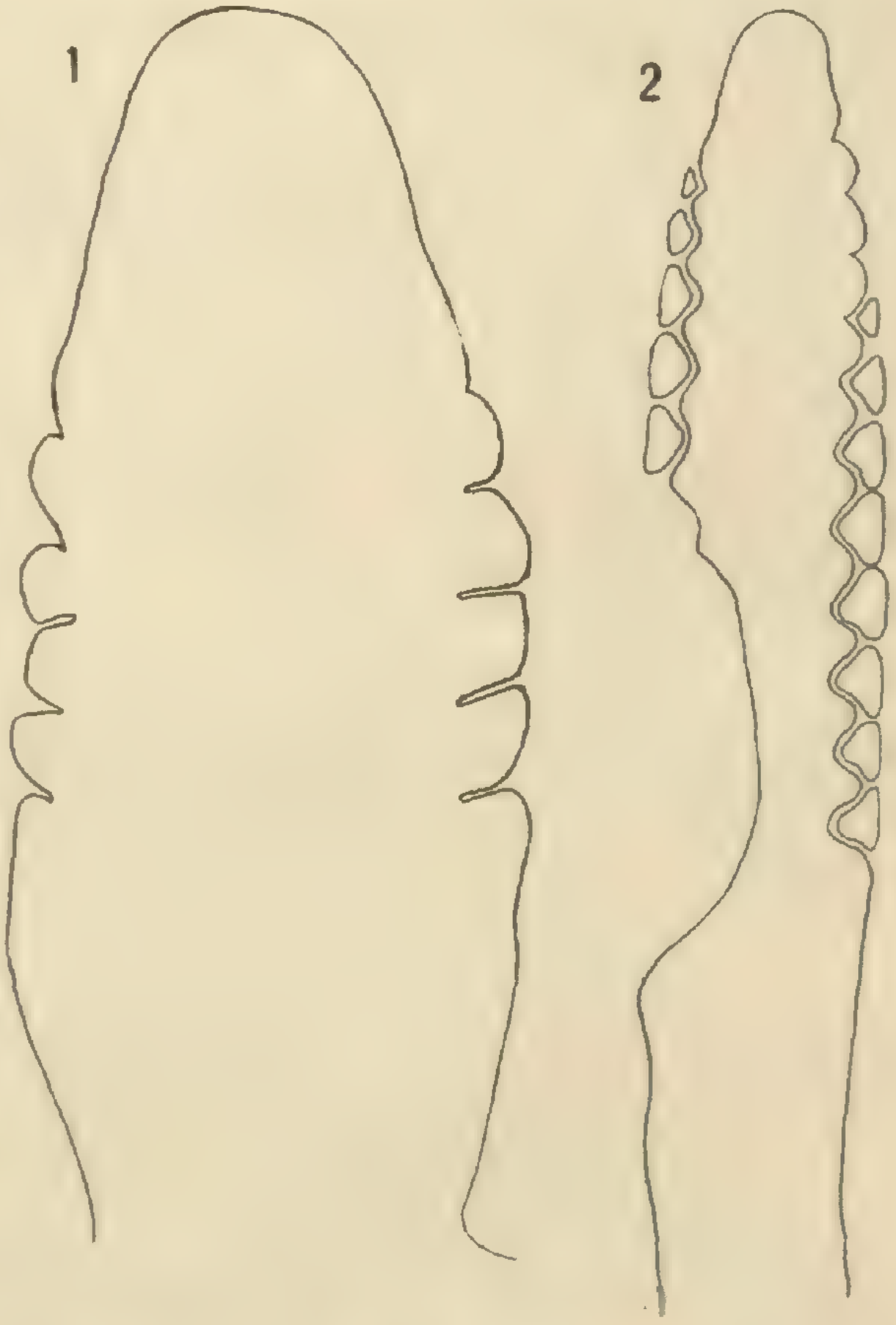
Each year, since 1906, an attempt has been made to secure material which should give the origin of the integument. In 1907, out of eight or ten plants sent from Florida between July 25 and August 8, not one contained an ovulate cone. I do not know whether this was an unfruitful year or whether the collector was unfortunate in the plants he gathered. Another year, knowing just the period during which the material ought to be gathered, careful collections were made, but in every case the cones had reached a development two weeks ahead of that of the previous year, so that it is evident collections of *Zamia* must be made often and during long periods in order to obtain a full series.

The facts ascertained from the material cover the period from the appearance of the ovulate cone to the time when the developing endosperm has partially filled the embryo sac, and will be treated under three periods of growth.

1. Development of the strobilus and the sporophylls

Plants gathered early in June show a slight elevation which elongates to form the strobilus, but at this stage it is impossible to distinguish the ovulate strobili from the staminate. As stated in my description of the staminate plants (1), the strobili are deeply sunken in the tip of the crown and are completely covered by the bases of the rosette of leaves.

A strobilus of July 5 is about 5 mm. long, and at this time can be recognized as ovulate. There are defined in a median longitudinal section five sporophylls on a side (fig. 1). A comparison with a staminate cone of July 8, with eleven sporophylls on a side, gives approximately the same length, but greater breadth and larger sporophylls than those of the staminate cone (fig. 2).



FIGS. 1, 2.—Fig. 1, longitudinal section of young ovulate strobilus, showing sporophylls (July 5). ×40; fig. 2, longitudinal section of young staminate strobilus, showing sporophylls (July 8). ×40.

In comparing cross-sections of strobili of July 25, much the same points are noticed. A staminate strobilus (fig. 3) has on an average fourteen to sixteen sporophylls on a cross-section, while the ovulate strobilus (fig. 4) has seldom more than ten. A difference in the size of the sporophylls as well as of the strobili is seen also.

The development of the sporophylls is identical in the two strobili, at least in these early stages, except that the elevation representing the sporophyll in the ovulate strobilus is broader and includes more cells in a hypodermal position which are dividing periclinally. As the sporangia appear, there are fewer meristematic points on the ovulate

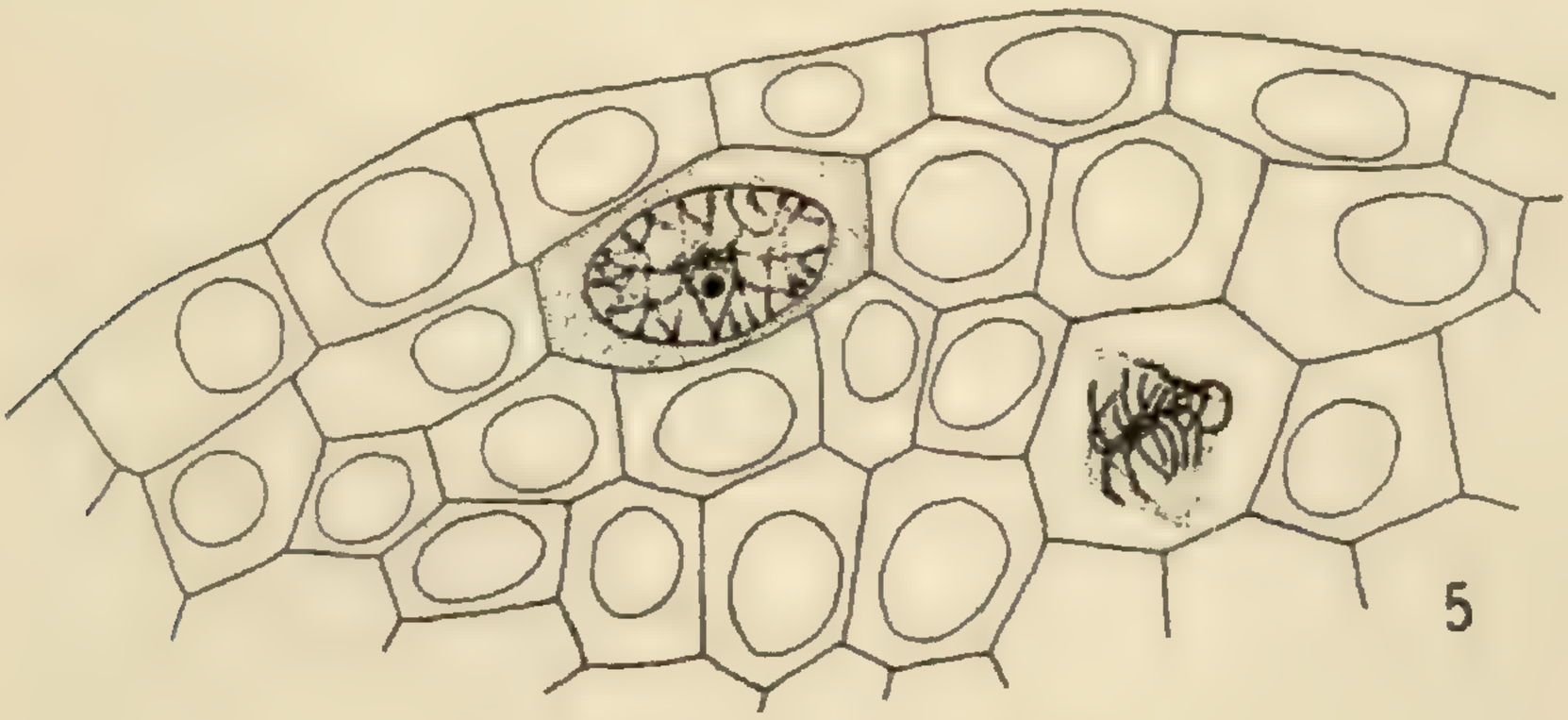
sporophylls, as shown in figs. 3 and 4. The lobes themselves are broader and the cells of the inner surface show a deeper stain, indicating that this is the region where active growth is taking place. This region is included by the dotted line drawn on one of the sporophylls in fig. 4.

In a megasporophyll of July 25, of the size in fig. 4, a cell can be distinguished for the first time from those about it by its size and

FIGS. 3, 4.—Fig. 3, transverse section of staminate strobilus, showing sporophylls and position of sporangia (July 26). ×40; fig. 4, transverse section of ovulate strobilus (July 26), showing sporophylls and meristematic group of cells on one lobe indicated by dotted line. ×40.

by its larger nucleus with deeply staining chromatin. This cell is hypodermal in origin (fig. 5) and resembles the single archesporial cell in the staminate sporangium. About ten or twelve cells in a cross-section form a meristematic group, some of which are actively dividing, but this archesporial cell is easily distinguished from these. In another sporophyll of July 25, but evidently one a little more developed as shown by its increased size, the development of this group of cells has gone on still farther, and now four cells in cross-section can be clearly distinguished from the others (fig. 6). This group is separated from the epidermis by one layer of cells, and the

size of its nuclei and the position of its walls suggest an origin from a single archesporial cell. It resembles, too, the group in the staminate strobilus which gives rise to the sporogenous mass in the microsporangium. Two pairs of cells (*t*) just under the epidermis, from the



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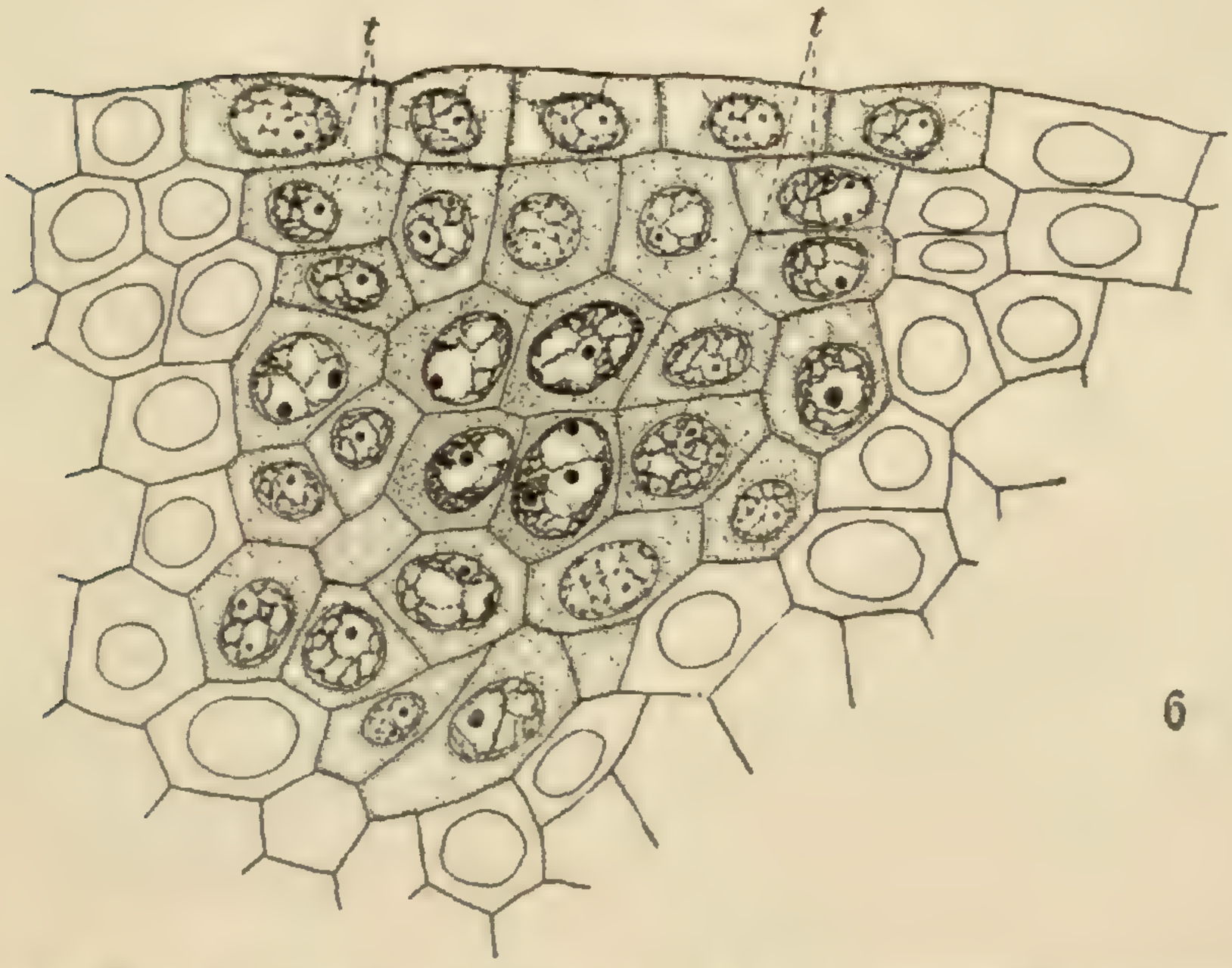

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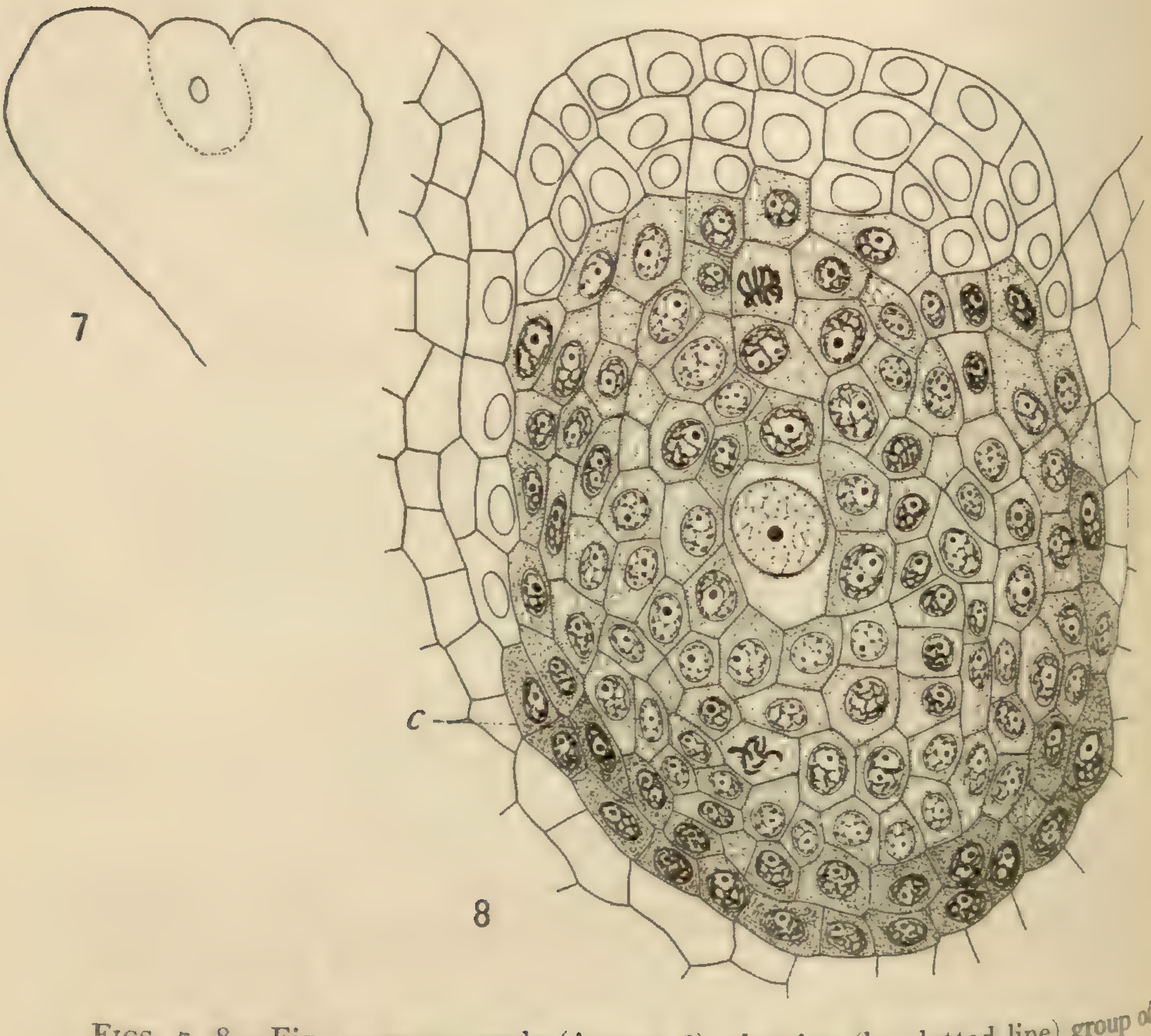
FIGS. 5, 6.—Fig. 5, detail of sporophyll of fig. 4, showing hypodermal archesporial cell. ×40; fig. 6, more advanced stage, showing group of meristematic cells (*t*) which may give rise to integument. ×1400.

direction of their walls indicate that they have arisen from periclinal divisions of hypodermal cells, and suggest the first divisions causing the elevation of the integument.

Just at this point there is the break in the continuity of the series referred to, and the strobili of August 8, which is the date of the next collection, show on either lobe of the sporophyll the projecting nucellus and the integument, which is only slightly elevated at this time.

2. Development of the ovule

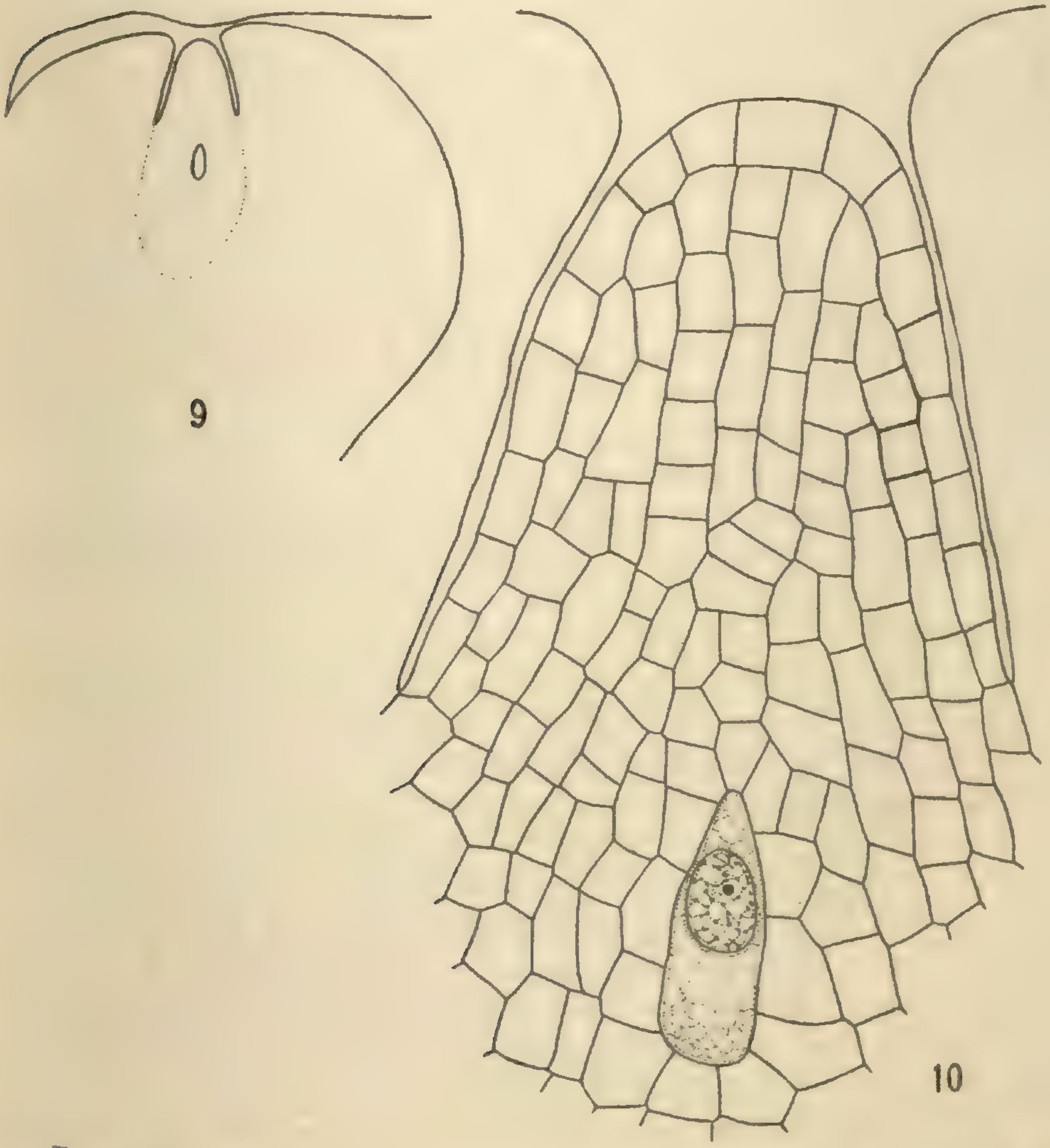
The ovule of August 8 shown in figs. 7 and 8 is younger, I think, than that of *Stangeria* as figured by LANG (**2**), and about the same age as that of *Ceratozamia* shown by TREUB (**3**). The megaspore mother cell is easily picked out at this stage as a larger cell, which is



FIGS. 7, 8.—Fig. 7, young ovule (August 8), showing (by dotted line) group of cells arising from archesporium. ×136; fig. 8, detail of fig. 7, showing megaspore mother cell, adjacent tissue dividing, and flattened cells (*c*) bounding nucellus. ×

more vacuolated and which has a large nucleus with the chromatin arranged in a fine network. The cells about it stain rather more deeply, and toward the chalazal end there are several rows of flattened cells (*c*) which stain still more deeply, and which form a boundary to the ovule in this direction. These rows curve up about the "sporogenous group" and meet the epidermis at the point where the integument and nucellus are separated from each other.

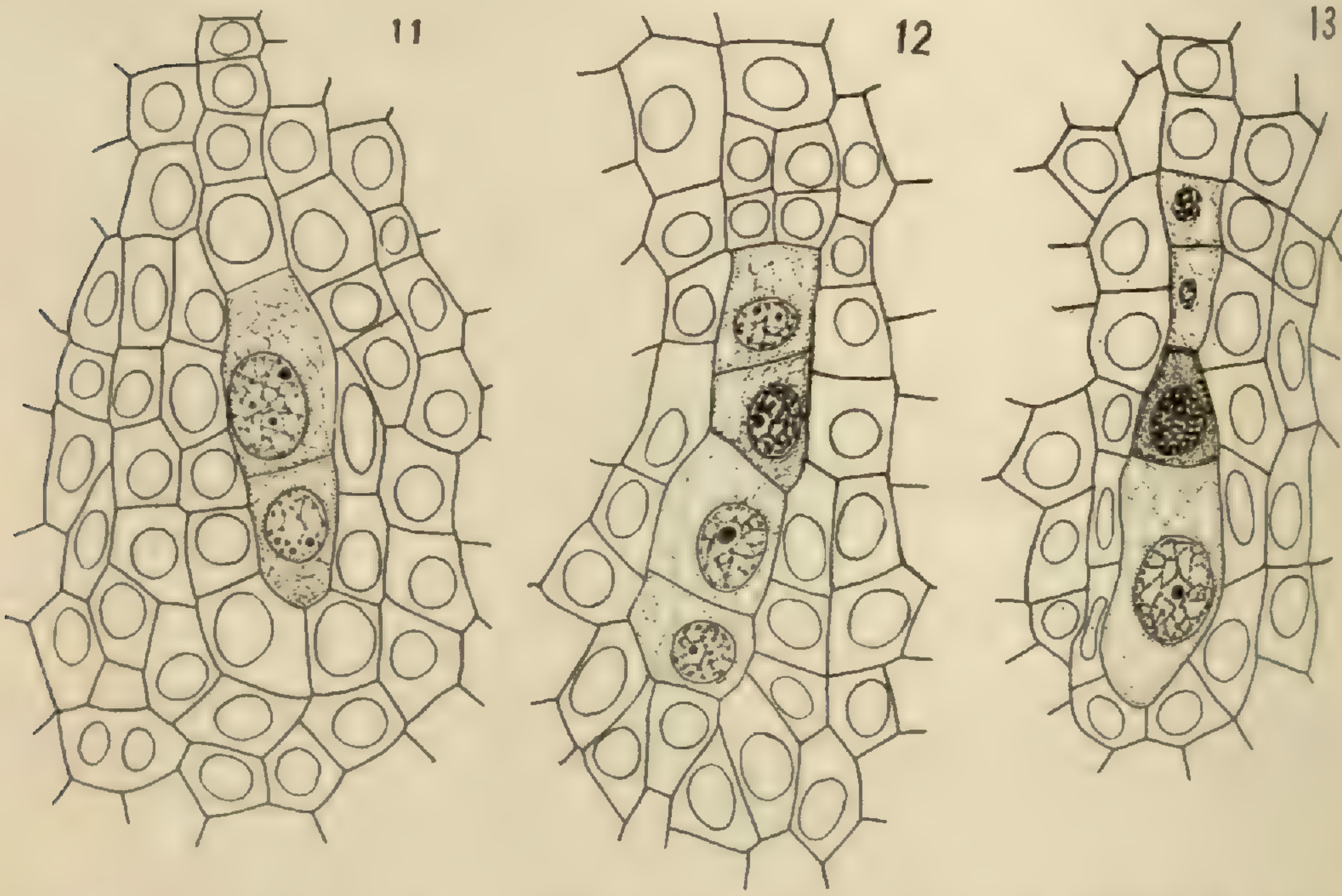
In the region of the nucellar apex, the cells are constantly dividing as the nucellus increases, but this cell activity is not confined to that part of the ovule. On either side and below the mother cell there is constant division, as is shown in sections through the mother cell



FIGS. 9, 10.—Fig. 9, older ovule, showing megaspore mother cell. ×136; fig. 10, detail of fig. 9, showing large increase in nucellar apex. ×930.

and in sections adjacent to it. Often there are three spindles in a section 8 μ thick. This megaspore mother cell enlarges somewhat before dividing again, while the nucellus by repeated periclinal divisions (figs. 9, 10) is becoming extended. This changes the broad, flat outline of the projecting portion to a narrower, more pointed one. The integument keeps pace in its development and narrows

the micropyle by growing in the direction of the nucellus. During this change in the nucellus the mother cell divides (fig. 11) into an upper larger and a lower smaller cell. The next stage seen (fig. 12) had a row of four megaspores, and the position of the upper two and again of the lower two would indicate that they were derived from these first two cells by a further division. Fig. 13 shows a disappearance of the two upper cells, indicated by the small nuclei and the

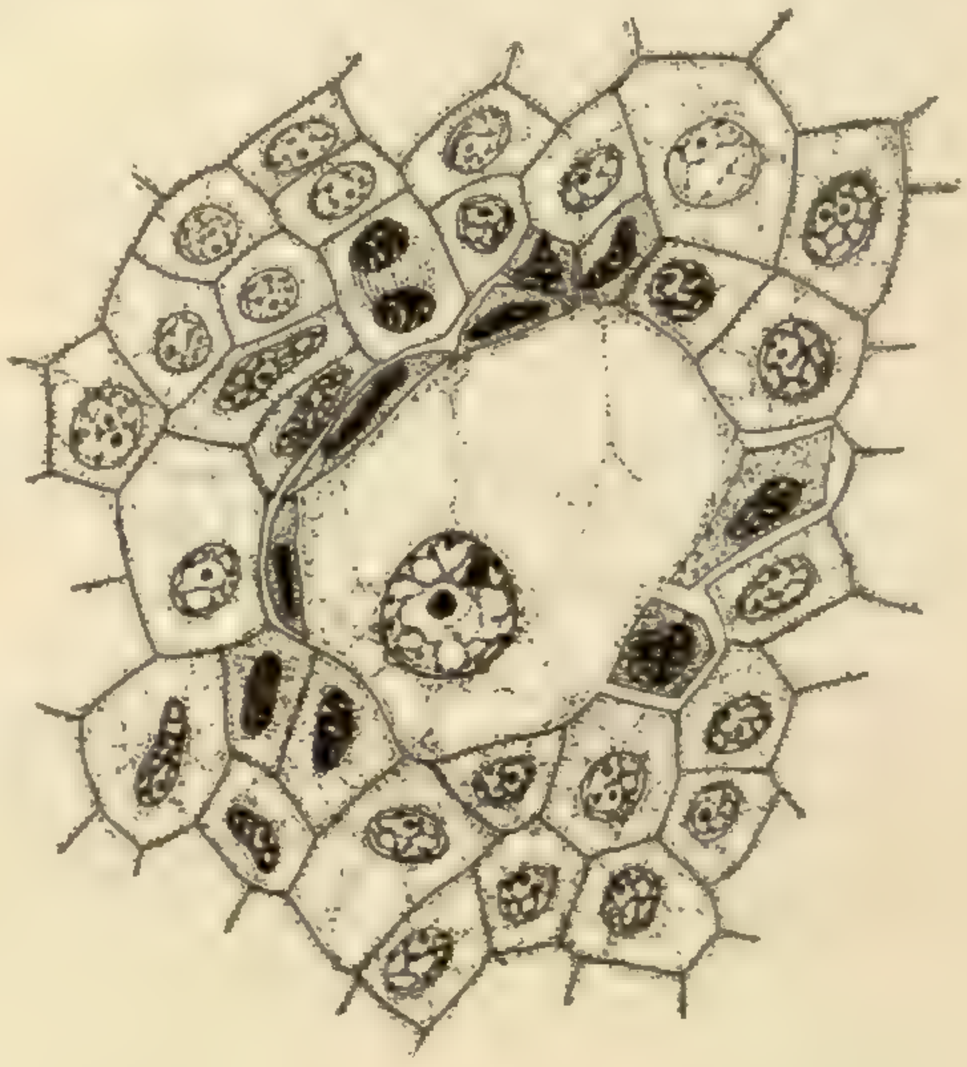


FIGS. 11, 12, 13.—Fig. 11, two cells arising from megaspore mother cell; fig. 12, chain of four megaspores. ×930; fig. 13, four megaspores: three degenerating, the fourth the embryo sac. ×930.

narrowed effect of the cells themselves. The nucleus of the cell just over the basal one of the chain is being flattened and crushed by the development of its sister cell, which is to be the embryo sac. In other sections there is a deeply stained cap over the micropylar end of the embryo sac, which is probably the remnant of the other megaspore or megaspores; at last this also disappears. From this time on the embryo sac enlarges rapidly and becomes more vacuolated (figs. 10, 14).

3. Development of the female gametophyte and changes in the "spongy tissue"

Many slides show the uninucleate condition of the embryo sac, indicating that this stage is quite prolonged. Fig. 14 shows a few cells surrounding the embryo sac, which are broken down by the growing sac; material killed August 29 is about the first to show this condition. The nucleus of the embryo sac divides as is described for other species, and the nuclei take the polar position. There is a slight indication of cytoplasm forming a lining to the wall, but the karyokinetic figure in the section drawn must have formed a little to the



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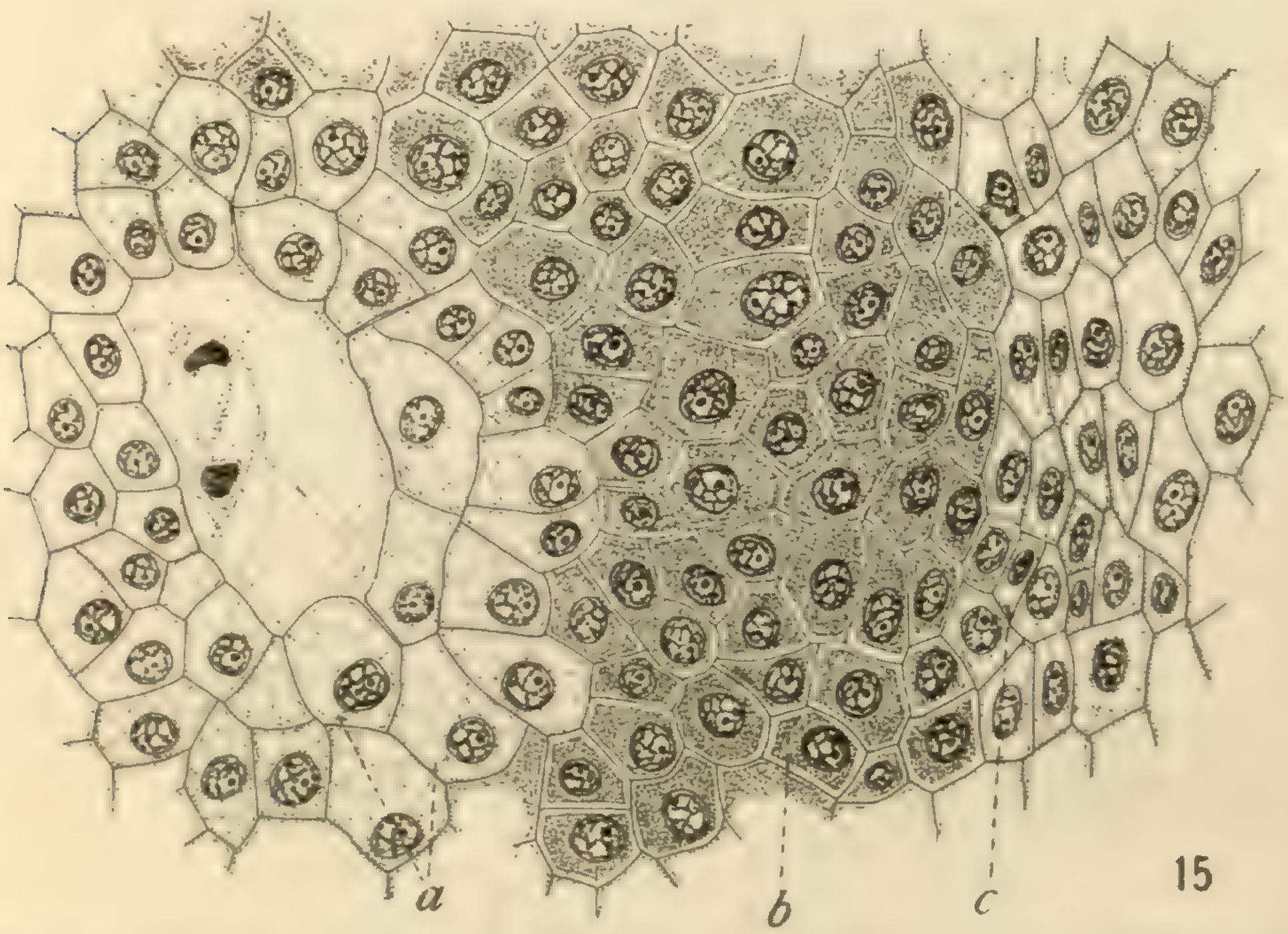

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FIGS. 14, 15.—Fig. 14, detail of enlarging embryo sac. ×930; fig. 15, detail of embryo sac and "spongy tissue" (August 29): *a*, active nutritive cells; *b*, tissue of closely packed cells; *c*, flattened cells bounding group. ×930.

side of the middle of the sac (fig. 15). Fig. 15 shows the sac and the surrounding cells on one side as far as the flattened rows (*c*)

forming the boundary of the group of cells which we may call the "spongy tissue," using STRASBURGER'S term. These flattened cells of the periphery were first seen in the young ovule (fig. 8). The "spongy tissue" may perhaps be referred to the mass which originated in a single archesporial cell, but the lack of sufficient material prevents me from drawing conclusions.

By the time the embryo sac nucleus has divided, the "spongy tissue" shows differentiation. Next to the embryo sac membrane the cells (*a*) are larger, more vacuolated, and often bulge into the sac as pressure is released on this side. Occasionally these cells are broken apart and the walls are very indistinct. The next rows (*b*), often eight or ten in number, are made up of smaller cells, therefore seeming to be closely packed and often dividing in such planes that they form rows radiating from the center of the sac. The nuclei and cells themselves stain deeply, contrasting both with the inner layers mentioned and with the flattened peripheral rows (*c*). Quite often a spindle is seen in these cells, so that this is by no means a degenerating tissue. The cytoplasm in the preparations has separated from the walls a little, and the walls are "so transparent that the nuclei seem to be floating in cytoplasm (3), but I am convinced that this is due to a slow passage of the killing fluid into the tissue and the consequent shrinkage. Fig. 16 shows the two embryo sac nuclei at the poles, and fig. 17 has four nuclei in one section, one of which has not yet passed to the peripheral position. The interior of the sac in these sections has a beautiful vacuolate structure, and the "spongy tissue" has not changed appreciably.

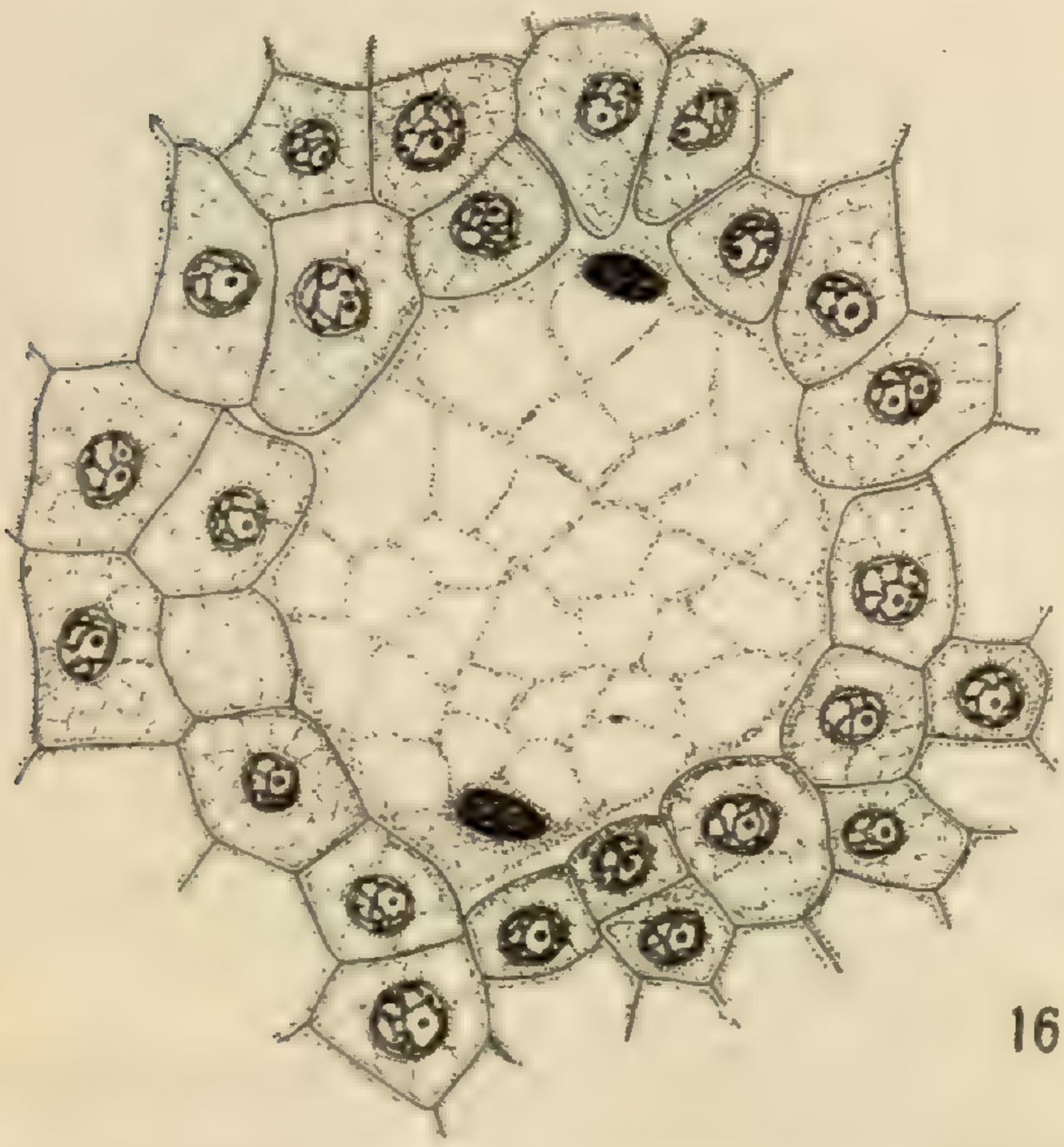
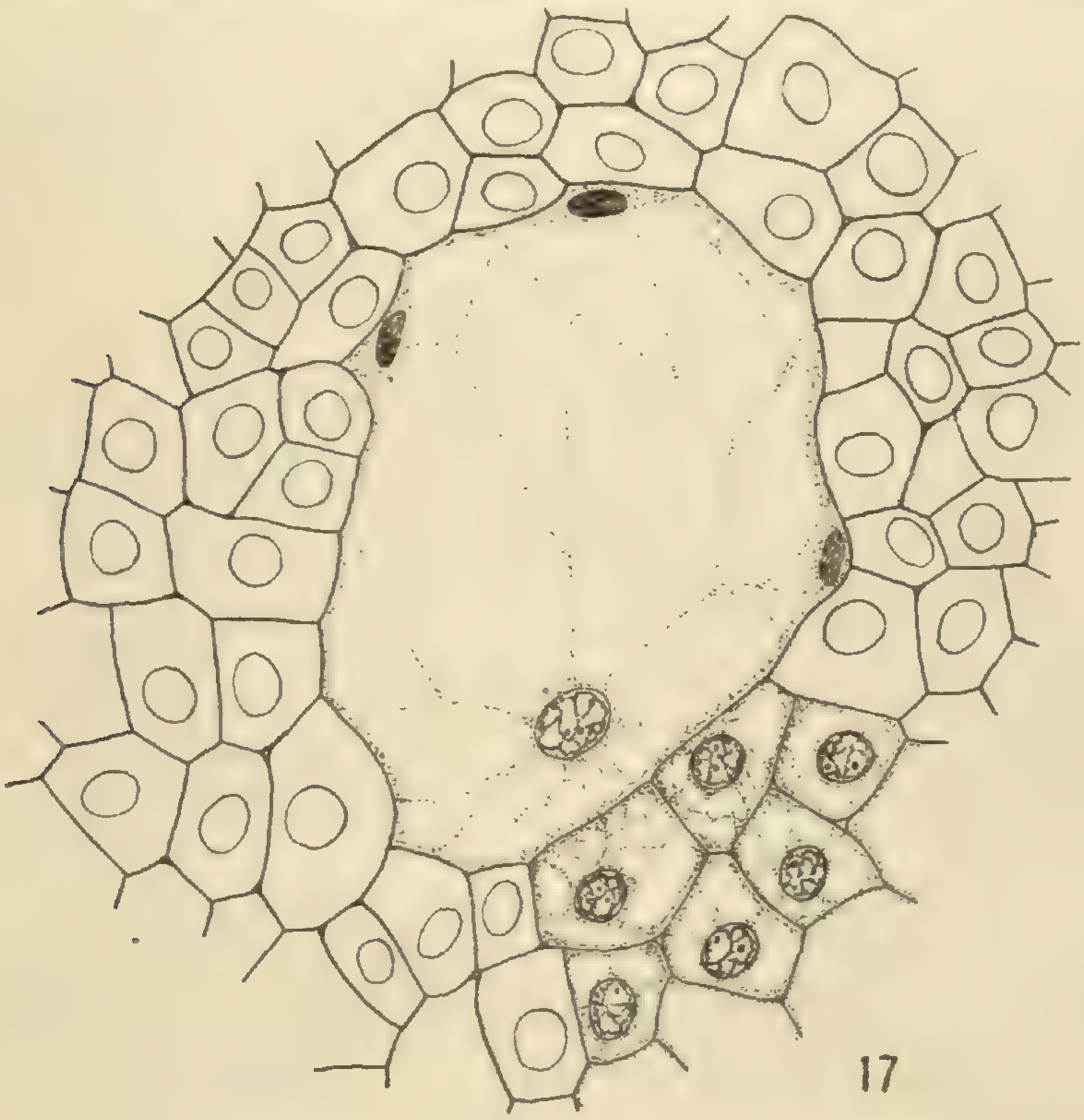
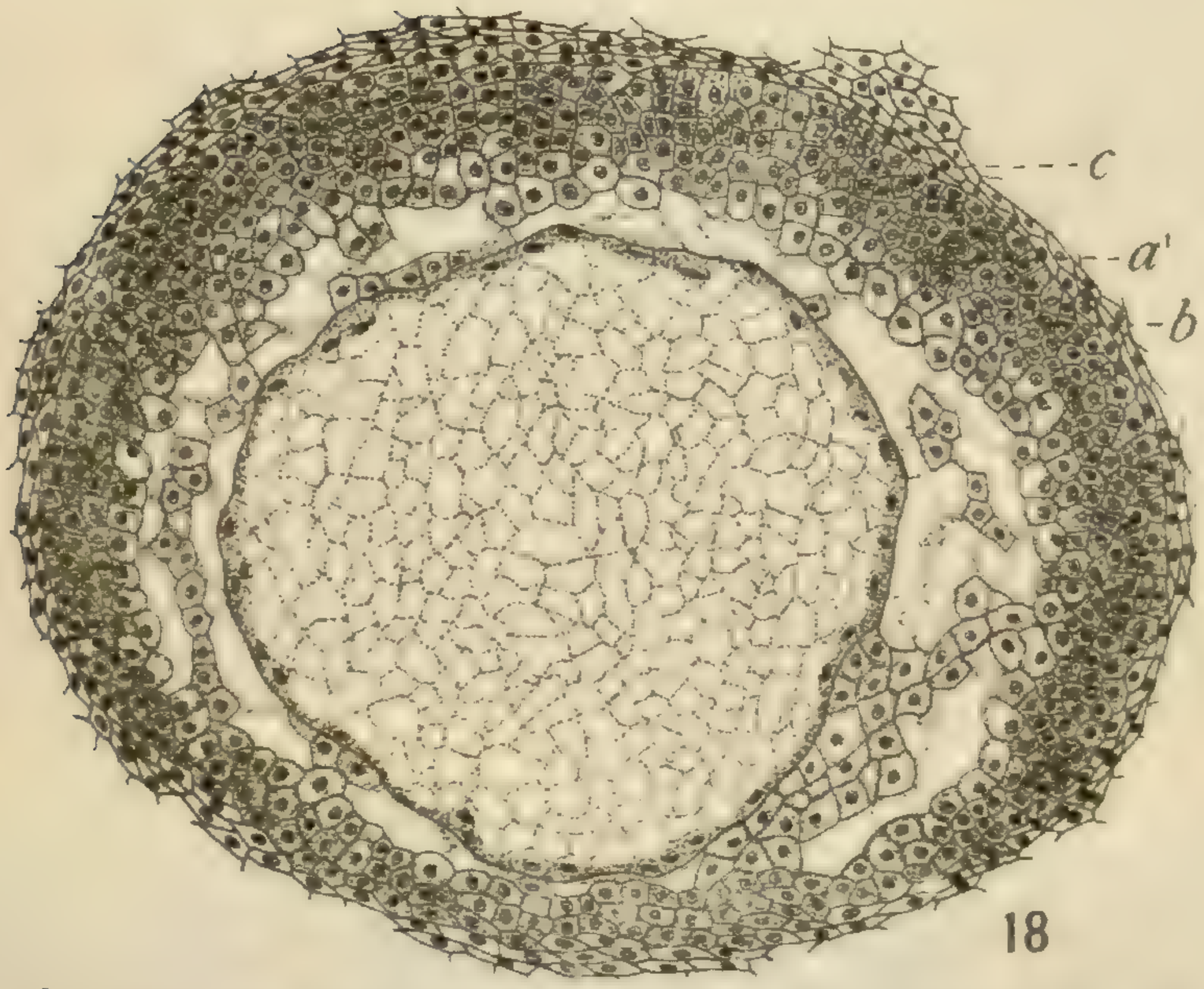


FIG. 16.—Polar position of embryo sac nuclei. ×930.

The next series of slides obtained give further divisions of free nuclei and their peripheral position in the cytoplasmic lining, which

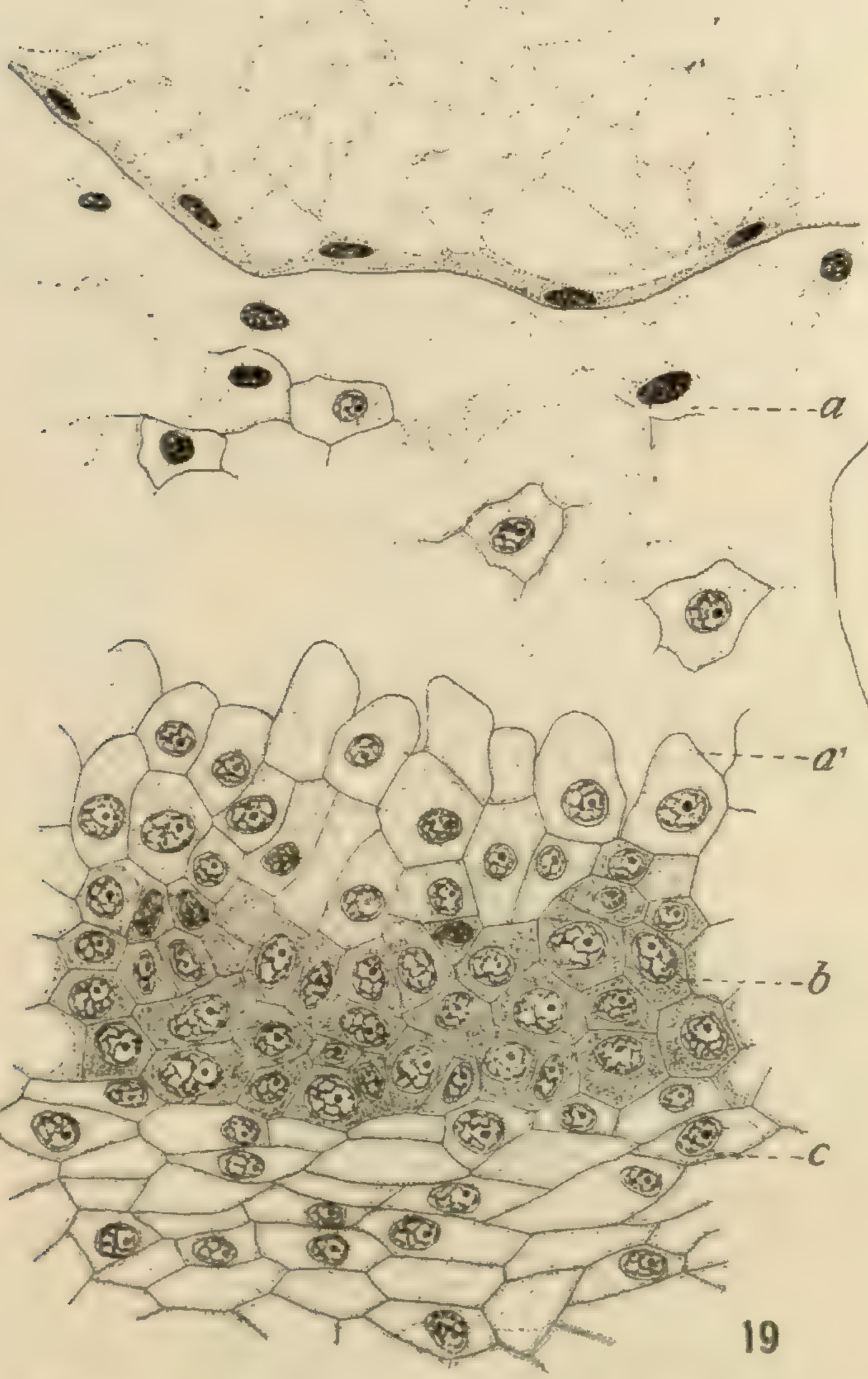




FIGS. 17, 18.—Fig. 17, four nuclei of embryo sac. ×930; fig. 18, embryo sac with layer of cells; spongy tissue beginning to break down. ×250.

is now a little thicker. The cytoplasm here is quite foamlike in its structure (figs. 18, 19). Fig. 19 is a detail of the sac and the "spongy

tissue" at the micropylar end. The result of the growth of the sac is seen in the breaking down of the "spongy tissue"; the layers nearest the sac are almost used up (*a*). Seemingly the wall of each cell is



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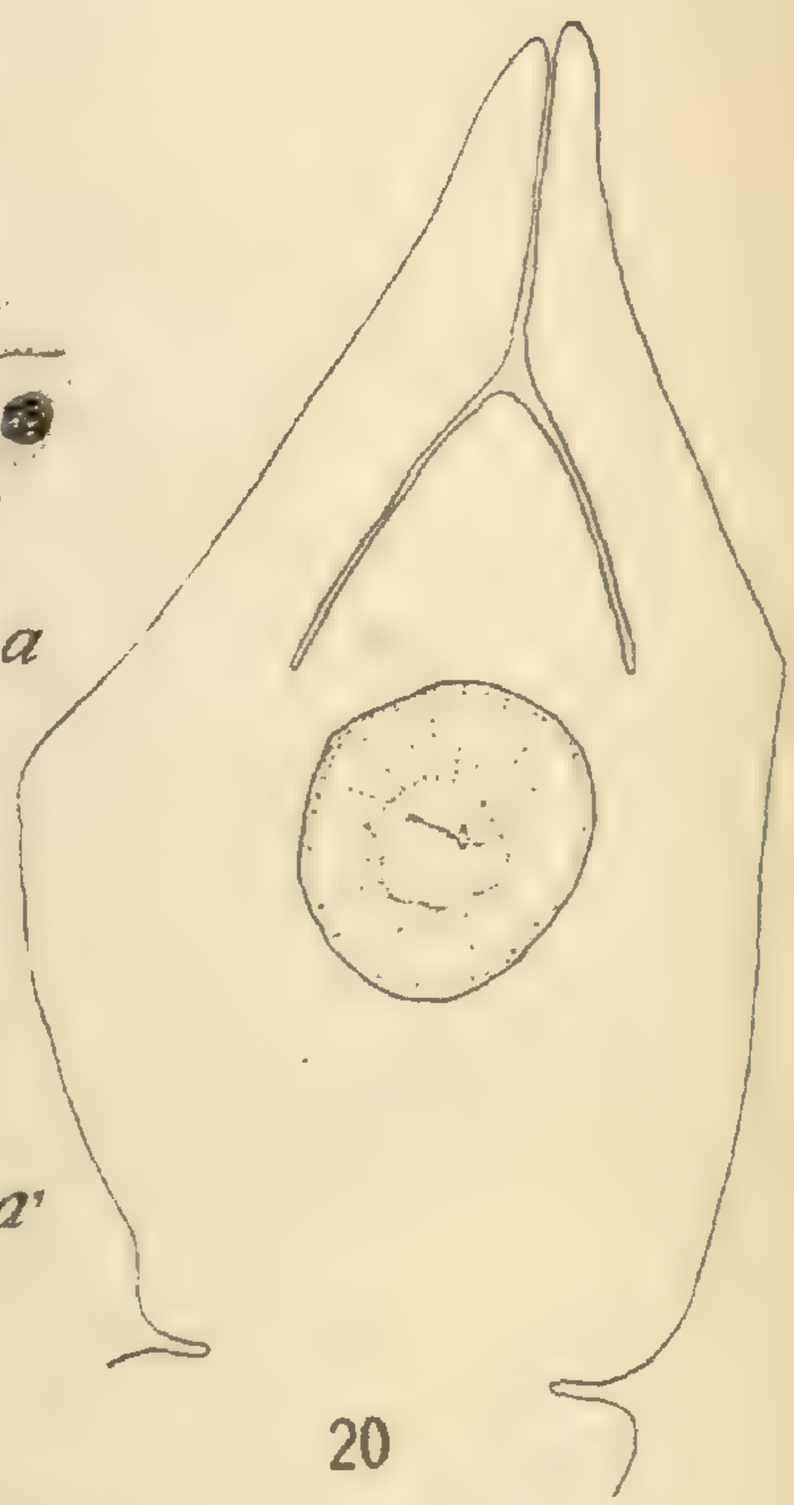

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FIGS. 19, 20.—Fig. 19, detail of fig. 18: *a*, "spongy tissue" broken down; *a'*, nutritive tissue; *b*, compact tissue; *c*, flattened cells. ×930; fig. 20, ovule showing unusual development of "spongy tissue." ×37.

attacked first, probably by an enzyme secreted by the developing gametophyte, and the cells become separated from each other. Sometimes a nucleus has its position in an isolated cell, and sometimes it is surrounded by cytoplasm. The breaking down of this tissue resembles that described by CHAMBERLAIN (4) in the formation of the pollen chamber of *Dioon edule*.

Next to this broken tissue there are several layers of cells (a') which resemble those in fig. 16 immediately surrounding the sac. These are swollen and have every appearance of being active, nutritive cells. Beyond this again is the deeply staining tissue (b), but narrower now, as if some of the cells had changed in their appearance and had taken

FIG. 21.—Detail of fig. 20. ×250.

on the function of the cells which previously bordered the sac. This tissue is narrower still toward the chalazal end of the sac.

Figs. 20 and 21 were made from an ovule in which the embryo sac was shrunken badly, but the amount of "spongy tissue" formed was unusually large and compact. The outer part shows radiation in its cell rows, as in other earlier stages. In one case this increase of "spongy tissue" was so great that it almost filled the interior, and the embryo sac had not developed. All these facts point to an active "spongy tissue" such as Miss FERGUSON claims for *Pinus* (**5**), and not

one which is formed early and which disappears early, leaving only a few thin layers, called "tapetum" by LANG (**3**) and not explained.

In fig. 22 this encroachment upon the "spongy tissue" has gone on until only about three or four rows are left between the sac and the bounding narrow cells (*c*). These inner cells have enlarged many times, as is shown by the magnification of the figures recorded. The walls of these cells (*b*) have become quite thick, the cells are full

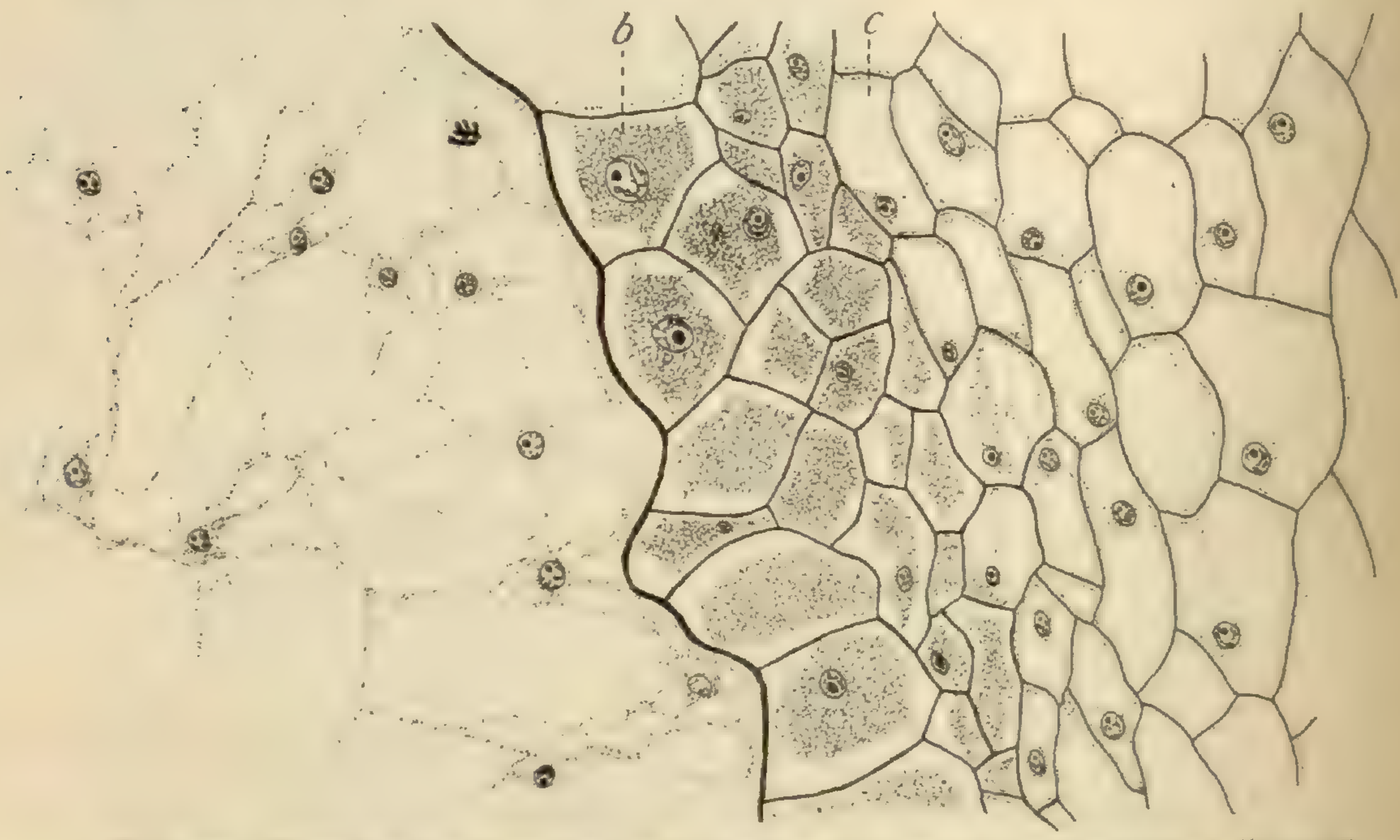

FIG. 22.—Detail of embryo sac with many free nuclei; diminished "spongy tissue"; cells of tissue (*b*) have increased in size and assumed nutritive function; *c*, flattened cells. ×580.

of cytoplasm, and the nuclei are not large, though not disorganized. The sac has now a broad cytoplasmic layer and a heavy wall. The nuclei are scattered everywhere, but have no walls as yet; at least none were seen in a careful examination with a $\frac{1}{12}$ oil immersion lens. The membrane is drawn away from the "spongy tissue" for a little distance at the micropylar end, so that in cutting the ovule it looks as if this end of the sac was not filled in.

From this stage on, the history of the development of the sac has been fully worked out in other forms by WARMING (**6**), whose description of the endosperm formation is excellent, by IKENO (**7**), and by others, so that it did not seem worth while to examine later material, at least not until the gaps behind could be closed up.

Summary

1. The young staminate and ovulate strobili can be distinguished by the difference in breadth, number of sporophylls, and number of meristematic points.

2. There is probably a single archesporial cell giving rise to a group of cells, one of which becomes the megaspore mother cell.

3. There are four potential megaspores, the lowest one becoming the embryo sac, whose development agrees with the accounts of other cycads in the main points.

4. The "spongy tissue" is an active, nutritive tissue, adding to its width by division of its cells as it is encroached upon by the embryo sac.

5. In its final degeneration, the cells of the "spongy tissue" nearest the embryo sac are first attacked, and the smaller cells outside them take their place, becoming large, swollen, and nutritive in function.

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OXIDIZING ENZYMES AND THEIR RELATION TO "SAP STAIN" IN LUMBER[1]

IRVING W. BAILEY

The discoloration of sap wood, or "sap stain" as it is commonly called, involves the loss or the depreciation in value of large quantities of lumber annually. Therefore, with the continually increasing value of lumber and the necessity for greater economy in the utilization of wood, the problem of saving and using the sap wood as well as the heart wood of the tree increases in importance each year. In endeavoring to prevent the discoloration of sap wood it is of fundamental importance to discover what agency or agencies produce the stain, and to study their mode of activity.

So far as the writer has been able to determine, there are in general two agencies which produce the discoloration of sap wood. One of these, which is of frequent occurrence and of great economic importance, is a purely chemical reaction which takes place in green sap lumber upon exposure to the air (oxygen). This chemical discoloration occurs in many varieties of wood, and is well illustrated by the reddish yellow or rusty colored sap stain which occurs in the sap wood of alder, birch, and cherry, and by the blue colored sap stain which occurs in the sap wood of red gum (*Liquidambar*). When the freshly cut surfaces of these woods are exposed to the air, under favorable conditions of temperature and moisture, a chemical reaction starts which with varying rapidity produces a colored substance in the wood. Favorable conditions for sap-staining are found during warm weather, and optimum conditions during extremely hot, humid, summer weather, when lumber becomes discolored within a few hours. The examination of microscopic sections of this sap-stained lumber reveals the fact that the colored substance, produced by the chemical reaction, is most conspicuously developed in the wood rays and wood parenchyma cells, living tissues which are largely concerned in the storage and conduction of food in the wood. The

[1] Contributions from the Phanerogamic Laboratories of Harvard University. No. 26.

second agency which produces discoloration in sap wood is the activity of fungi, which find an abundant food supply in the sap wood, and under favorable conditions of heat and moisture (hot, humid weather) develop with great rapidity. Thus part at least of the blue colored sap stain which occurs so frequently in pine may be produced by the dark colored mycelium of a fungus which is found in the food-containing wood rays and the parenchyma cells surrounding the resin canals. In fact, in all samples of blue sap pine which have come under my observation the color has been produced by this dark colored mycelium. However, it seems very likely that a large part of the blue sap stain in pine is produced by chemical reactions, for I am informed by lumbermen that sap pine lumber frequently stains badly during a few hours. The rapidity with which the discoloration is produced indicates the activity of a chemical reaction.

Although the two agencies producing sap stain are so fundamentally different, yet the conditions which favor their activity are very similar. As has been indicated above, each agency, in its activity, is closely related to the food substances contained in the wood. This is shown by the fact that the discolorations, produced by the activity of fungi and by chemical reaction, are most conspicuously developed in the wood rays and wood parenchyma cells. Both agencies producing sap stain are, in addition, dependent upon certain quantities of oxygen (air), heat, and moisture. Thus optimum conditions for sap-staining are found in green sap lumber during hot, humid weather, whereas unfavorable conditions are found in cold, dry weather and in logs immersed in water. It is well known that certain quantities of food, oxygen, moisture, and high temperature are necessary for the rapid development of fungi, but it seems advantageous to examine with greater care a chemical reaction which is dependent upon similar conditions.

Oxidizing enzymes

It has been known for many years that certain soluble ferments, which facilitate the oxidation of organic compounds, are widely distributed in plants and animals. These oxidizing enzymes are of fundamental importance in the nutrition and growth of living organisms. Furthermore, it has been clearly demonstrated that these enzymes

produce certain striking postmortem changes in animal and plant tissues. I refer in particular to the postmortem discolorations of certain organic compounds which are produced by the oxidizing activity of these enzymes. The most striking illustration of this oxidation and discoloration in plants was pointed out, in 1883, by a Japanese, HIKOROKURO YASHIDA, who discovered that the formation of black varnish by the oxidation of the latex of the lac tree was produced by the intervention of an oxidizing ferment. Since this discovery, the activity of oxidizing enzymes has been carefully studied in the discolorations which are produced by them in the extracted juices of fruits, vegetables, cereals, mushrooms, and other soft plant tissues. These investigations have shown conclusively that, as in the case of the oxidation of the latex of the lac tree, postmortem discolorations are produced in these juices by the intervention of oxidizing ferments. This change of color which is produced in the extracts of plant tissues has been used as the basis for very delicate tests for oxidizing ferments. A strong blue color produced in an alcoholic tincture of guaiacum, in the presence of oxygen or hydrogen peroxid, indicates the presence of oxidizing enzymes. Upon the basis of these tests certain authorities divide oxidizing ferments into oxidases and peroxidases, according to whether the blue color produced in the tincture of guaiacum occurs in the presence of oxygen or hydrogen peroxid.

It is of interest to note the behavior of oxidizing ferments under variations of temperature. Investigation has shown that optimum temperatures exist for oxidizing enzymes at which they react with great activity. Below these optimum temperatures their activity decreases, and similarly in increasing the temperature above the optimum their activity decreases, and in almost every case their activity is entirely destroyed before a temperature of 100 C. is attained. The activity of oxidizing ferments is also decreased or destroyed by certain antiseptics, and by other chemical substances.

From this consideration of certain properties of oxidizing enzymes, we see that there exists a strong similarity between their oxidizing activity and the chemical reactions which produce sap stain. In each case postmortem oxidization with change of color is produced by solutions in contact with the air (oxygen), and variations in tempera-

ture produce similar variations in the activity of the discoloring agency.

Prevention of sap stain

The fact that the temperature of boiling water destroys the activity of oxidases and peroxidases suggested to the writer the idea, that if sap stain were produced through the action of oxidizing enzymes, a simple method of preventing the discoloration of sap wood might be secured by immersing lumber in boiling water. During the spring of the present year the writer has tested this method on small boards (1″×3″×6″) of *Alnus incana* Moench., *Betula populifolia* Marsh., *B. papyrifera* Marsh., and various rosaceous trees. These species were selected as, at this latitude (Massachusetts), the sap wood stains very easily and rapidly during the spring upon exposure to the air, whereas the sap wood of such trees as sweet gum, maple, and basswood stain deeply during extremely hot and humid summer weather. The result of these tests has been to show that boards immersed in boiling water for a few minutes remain permanently unchanged in color, whereas untreated pieces stain rapidly and deeply. The fact that the unboiled boards stained on exposure to the air and that the discoloration was prevented by boiling offered strong evidence for believing that sap stain results from the action of oxidizing ferments. On testing boiled and unboiled boards with the guaiacum tests, the blue color produced in the unboiled boards demonstrated the presence of oxidizing enzymes.

In conducting these experiments the boards which were to be boiled and those which were to serve as controls were in all cases cut from the same part of the same tree, and were subsequently exposed to the same atmospheric conditions of temperature and humidity. The extreme sensitiveness of oxidizing enzymes in their oxidizing activity was clearly demonstrated by the species of wood used in these tests. For example, alder and birch, which in hot, humid weather stain in a few minutes to a reddish yellow or rusty color, stain more slowly at lower temperatures, and in cold dry weather stain but slightly even after an interval of several weeks. In a similar way the depth to which the stain penetrates into the wood varies with temperature and moisture. Boards dried in sheds stain superficially,

whereas boards dried in damp conditions in the open stain very deeply and densely. Boards treated in hot water and dried under cover remain unchanged in color throughout, and those placed in the most unfavorable conditions of abundant moisture and high temperature in the open, although they scorch superficially, as does all lumber exposed to the direct rays of the sun, remain unstained beneath this thin layer of tan.

Practicability of hot water treatment

It will occur to some readers that the activity of oxidizing enzymes could be prevented by kiln drying or steaming the wood, and that one of these methods would be more practicable than immersion in boiling water. However, to those familiar with saw mill practice it is evident that in mills sawing many thousand board feet of lumber each day and night it is usually difficult to steam or kiln dry more than a small percentage of the cut. Steaming or kiln drying are expensive processes, and the latter can only be applied to certain varieties and grades of wood. Furthermore, these processes are time consuming and require much handling of the lumber. Some method must be devised for preventing sap stain which can be carried out very cheaply and rapidly, in order not to interfere with the movement of the lumber from the saw to the yard. In other words, the lumber must be removed, treated, and piled as rapidly as it is sawed, in order not to interfere with the daily output of the mill. Some of the larger mills in the south have installed tanks containing chemical substances which destroy the action of oxidases and prevent discoloration by fungi. The lumber as it comes from the saw is carried through this tank upon carrier chains and thus immersed and coated with the chemicals. Certain difficulties have been encountered in the use of this method. One of the most serious is the fact that the chemicals used fire proof the outer surface of the boards, and when the treated lumber is shipped to northern markets for finishing the planings and shavings cannot be burned. This obliges the use of coal to run the planers and other machinery, and the non-combustible planings must be disposed of.

In the treatment of lumber with boiling water a similar method could be employed. Long shallow tanks in which water is heated

by steam pipes or by steam exhausts could be arranged so that the lumber from the saw could be passed through the tanks on carrier chains.

During the coming summer the writer will extend his experiments to include a wider variety of woods, and will conduct experiments of a practical nature in a large southern saw mill, to determine the relative advantages of hot water treatment and treatment with chemical substances.

Summary and conclusions

1. Sap stain is in general produced in two ways, by the attacks of fungi and by chemical discoloration.

2. Chemical discoloration is produced in sap wood by the activity of oxidizing enzymes.

3. Hot, humid weather is very favorable to the activity of these ferments, and cold winter weather is unfavorable.

4. Oxidizing enzymes which produce sap stain in wood are destroyed and their oxidizing action prevented by a temperature of 100° C.

5. Treating the sap wood of alder, birch, and cherry with boiling water destroys the oxidizing enzymes in the wood and prevents sap stain.

6. Treating sap lumber in long tanks of boiling water appears to be a practical method of preventing sap stain, and to be well adapted to saw mill practice.

In conclusion the writer wishes to express his sincere thanks to Professor E. C. JEFFREY for valuable assistance in carrying out this investigation, to Professor G. E. OSTERHOUT for advice and suggestions, and to MR. W. R. BUTLER for material of sap-stained lumber.

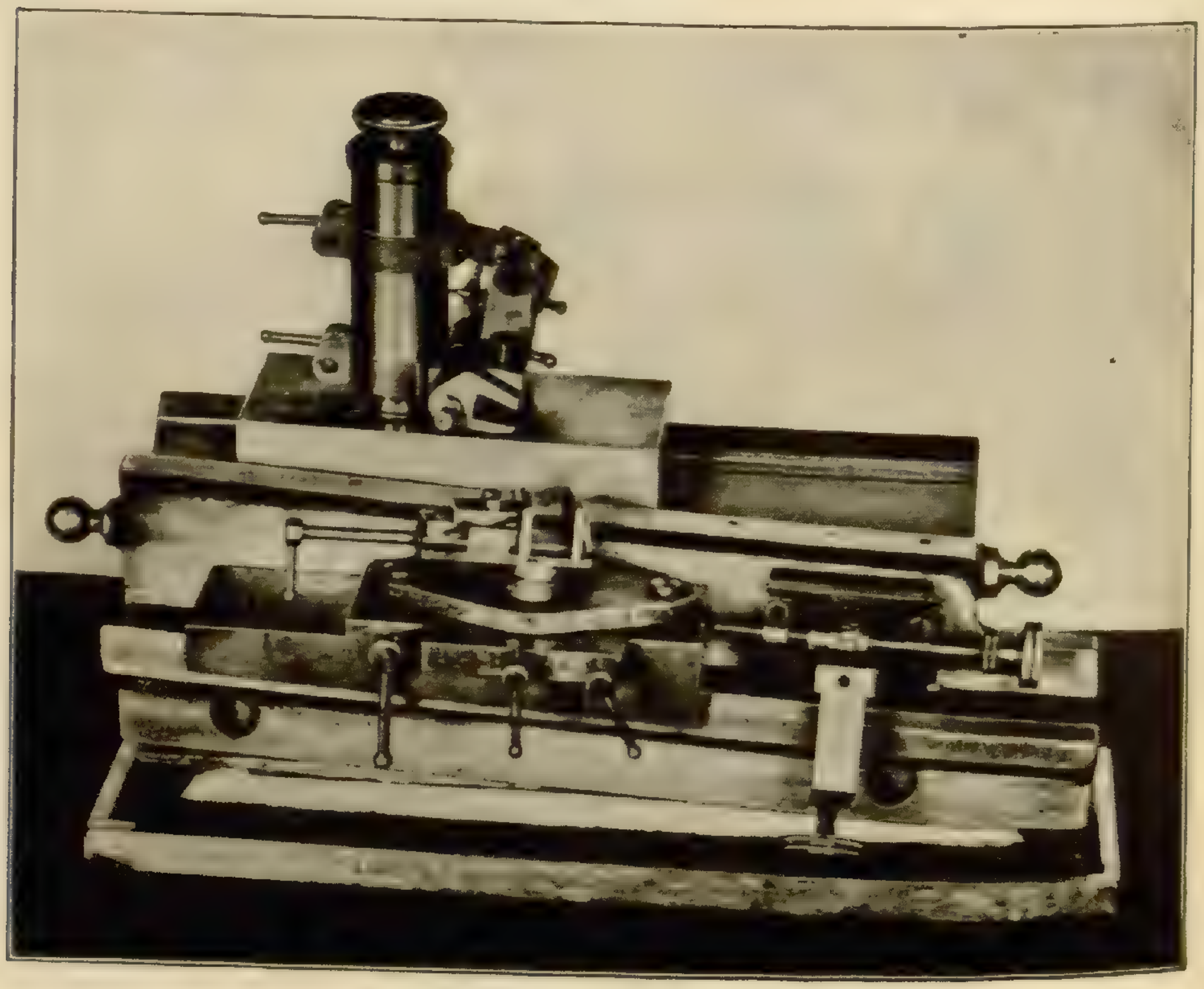
HARVARD UNIVERSITY

BRIEFER ARTICLES

A MODIFICATION OF A JUNG–THOMA SLIDING MICROTOME FOR CUTTING WOOD

(WITH ONE FIGURE)

The object and knife carrying blocks are long and heavy. These have planed surfaces of contact with the running surfaces of the base, instead of being mounted on ivory bearings, as is the case in the Thoma instrument. When oiled, the blocks are held by capillarity so firmly to the tracks that



the whole instrument can be suspended by either block without breaking the contact. In this way rigidity is secured and vibration eliminated, so far as the running surfaces are concerned. The friction of running is less than in the ordinary Thoma.

The object clamp is mounted on a solid ball (1.25 inches diameter), in a tight socket. This ball can be revolved horizontally through 180° and vertically through about 45°. It has two orienting levers whose axes

of contact with the ball are at right angles to each other, so that *definite orientation* of the object in either of *two* planes is possible. A third lever draws the plate which fits around the "shoulder" of the ball down when correct orientation has been attained, and makes the whole absolutely rigid.

The knife carrier revolves horizontally on the column of the knife block, and is rapidly adjustable to a height of 1.25 inches by means of the screw at the top, the two levers behind clamping it instantly in place. Arrangement has also been made for the adjustment of the vertical angle of the knife.

The rigidity and rapidity of the adjustment of this instrument are found invaluable in cutting many and long series of wood sections. Its usefulness was demonstrated in the sectioning for Mr. W. P. THOMPSON'S work on the rays of the conifers recorded in this issue of the BOTANICAL GAZETTE, and the structure of the instrument is outlined here in the hope that others may find it useful.

No small amount of the credit for the performance of the instrument is due to the excellent workmanship of Mr. H. W. SPENCE, who also assisted in the designing.—R. B. THOMSON, *University of Toronto.*

CURRENT LITERATURE

BOOK REVIEWS

The oxidases

KASTLE[1] has recently published a monograph on oxidases and other oxygen catalysts concerned in biological oxidations. The work is a compilation of our present knowledge concerning oxidases and other oxygen catalysts, as well as an excellent historical résumé of the subject. The constantly growing recognition of the important rôle of oxidases and related oxygen catalysts in biological processes, as well as the rapidly growing literature on the subject, makes a summary of the real contributions especially valuable at the present time.

The first chapter deals with the important past and present theories of oxidation, beginning with SCHOENBEIN'S ozone theory. After a brief discussion of this theory, the author proceeds with a more detailed account of VANT' HOFF'S theory of ionization, HOPPE SEYLER'S nascent hydrogen theory, and the peroxid theory of TRAUBE, ENGLER, and BACH. The conception which involves an exchange of electrical potential in oxidations, however, is not mentioned.

The second chapter takes up the oxidizing ferments, and begins with a discussion of their rôle and range in biochemical processes. This is followed by a detailed account of the guaicum reaction, since our first knowledge of oxidizing ferments is so closely associated with the reaction. The historical treatment of oxygen exciters and oxygen carriers is divided into two periods. The first covers the first sixty years of the nineteenth century, with SCHOENBEIN'S contributions standing out as the most important. He supposed that by means of various substances and under various influences the oxygen of the air becomes ozonized. These substances may in turn combine with ozone thus produced to form an active ozonid, which in turn can give up its oxygen to other less readily oxidizable substances. Thus the presence of oxygen activators and carriers was recognized, and the most important characteristics of oxidases and peroxidases discovered, although up to this time these terms had not been introduced into science.

During the second historical period, the contributions of TRAUBE and BERTRAND are especially emphasized. TRAUBE in his *Theorie der Fermentwirkungen* (1858) established the chemical entity of oxidizing ferments and their importance in acting as chemical go-betweens between free or combined oxygen

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[1] KASTLE, J. H., The oxidases and other oxygen catalysts concerned in biological oxidations. U.S. Public Health and Marine Hospital Service, Hygienic Laboratory. Bull. 59. 1909.

and the fermentable substances. To BERTRAND we owe the introduction into science of the term oxidase. The adoption of this general term was based upon the discovery and characteristics of laccase and tyrosinase. The chapter concludes with a classification of oxidases and special reference to the sources, preparation, and characteristics of laccase, tyrosinase, aldehydase, and the purin oxidases.

The third chapter is devoted to the peroxidases and catalases. The weight of opinion is inclined to the conception that peroxidases are substances capable of forming unstable peroxids from hydrogen peroxid, by double decomposition or by combining directly with the hydrogen peroxid to form unstable holoxid (TRAUBE) derivatives, possessing greater powers of oxidation than hydrogen peroxid.

BACH and CHODAT'S conception of an oxidase consisting of a mixture of peroxidases and peroxid-forming substances (oxygenases) would make the peroxidases the more important agents in plant and animal oxidations, and would relegate the oxidases to an insignificant position in such oxidations, if indeed they function as enzymes at all. In the author's opinion the objections which have been recently urged against the true enzymatic nature of oxidases are well taken.

A considerable amount of evidence is brought together to show the importance of iron, copper, and manganese as coenzymes to oxidizing ferments. According to BERTRAND, manganese is the really active element of the oxidases, so far as the activation and transfer of oxygen is concerned. EULER and BOLIN have found that laccase has no action on hydroquinone in the absence of manganous salts, and therefore they suggest that laccase owes its activity to the presence of such salts. In this connection it is interesting to note that in a paper by BACH,[2] more recent than the above monograph, he claims to have obtained a tyrosinase which will oxidize tyrosin to the red stage and is free from both iron and manganese. He concludes, therefore, that manganese and iron salts are in no way necessary for oxidase activity. One of the most valuable features of the monograph is the comprehensive list of references to the literature.—CHARLES O. APPLEMAN.

Colloidal chemistry

The newer plant physiology should welcome the appearance of FREUNDLICH'S book[3] on colloidal chemistry, or capillary chemistry, as he terms it. This is the first attempt to bring together our knowledge of this youngest and most difficult branch of physical chemistry. It puts the physiologist immediately in touch with the present status and most important literature of a subject which seems destined to play at least as important a rôle in the study of vital phenomena as

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[2] BACH, A., Zur Theorie der Oxidasewirkung. Ber. Deutsch. Chem. Gesell. **43**:362. 1910.

[3] FREUNDLICH, HERBERT, Kapillarchemie, eine Darstellung der Chemie der Kolloide und verwandter Gebiete. 8vo. pp. viii + 591. *figs.* 75. Leipzig. 1909.

has the chemistry of true solutions. The importance of surface tension in the mechanics of cell life has been emphasized, adsorption phenomena have recently become important in our consideration of semipermeability, selective absorption, etc., they must also be called upon to explain many of the relations between soil and plant. The student of protoplasmic structures, nuclear membranes, chromosomes, fibrillae, and the rest, is perhaps more familiar with coagulation of colloids and adsorption than he knows; his killing and fixing are examples of the former, while the whole process of staining apparently depends upon the different adsorptive powers exhibited by various portions of the coagulated protoplasmic mass. The so-called Brownian movement and the other phenomena of motion usually observed in the protoplasmic emulsion are likewise to be classed under capillary chemistry. If enzyme action is to receive an explanation, it bids fair to come also from this realm.

With this book and the field that it represents once in general use, it would seem that physiological research should receive a very great impetus along just those lines where it now wavers most. One of imagination, who appreciates the problems and present rapid advance of this and other branches of physical chemistry, should have little cause so thoroughly to lose heart as to need the aid of those "entelechies" and other *dei ex machina* with which the "neo-vitalism" seems to be somewhat overburdening biological philosophy. In the present exposition of capillary chemistry the author proceeds from the simpler phenomena of surface tension and capillarity to subjects of more complex nature, such as adsorption, colloidal solutions, suspensions, emulsions, catalysis, and the like. Every section is brief, clear, and directly to the point in hand; experimental evidence is given prominence rather than theoretical deductions, though the latter are not wanting; and numerous footnotes orient the reader in the scattered literature of the subject. An index of authors and one of subjects enhances the value of the work.—B. E. LIVINGSTON.

MINOR NOTICES

Insect galls.—Miss STEBBINS[4] has published a bulletin on insect galls of Springfield, Mass., and vicinity, which will be very useful to botanists who are interested in cecidology. The galls are grouped with reference to the plants, which have been arranged in accordance with BRITTON'S *Manual*. This is the first American work in which these pathological growths have been grouped with reference to the host plants. The record shows 204 species of gall-producing insects, which are distributed in 52 genera, 14 families, and 6 orders. The galls occur on 93 species of host plants, which are distributed among 48 genera, 29 families, and 16 orders. The descriptions of the galls are clear and are reinforced by 112 illustrations. The descriptions of the insects are omitted, but the synonomy and bibliography given with each will enable the student of entomology to look them up without difficulty. The galls of 26 new species are described and named,

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4 STEBBINS, FANNIE A., Springfield Museum of Natural History, Bulletin 2. 1915.

and 6 are described without names. The describing and naming of new species of galls without the insects has been the subject of considerable criticism, but since it gives us a definite record of these species the reviewer is inclined to favor the violation of this law of nomenclature. The work closes with an extensive bibliography, a systematic index of gall insects, and an index of scientific and common names of host plants.—MEL T. COOK.

NOTES FOR STUDENTS

Influence of environment on wheat.—One of the most persistent theories in evolutionary discussions of cultivated plants is that of the "breaking up of types," supposed to be brought about when plants are grown from seed under conditions differing markedly from those under which the parent plants were grown. Evidence for this view has been largely of an observational nature and capable of other interpretation. Experimental evidence bearing on the question has been brought out by LECLERC and LEAVITT[5] in reporting a series of cultures of wheat in widely different sections of the United States. The plan of the experiments was as follows: In one series Kubanka wheat grown in South Dakota was distributed to stations in Kansas and California, a sample being likewise grown in South Dakota. Every year a sample from each station was sent to each of the others and grown there. A similar series of cultures was carried out with Crimean wheat in Kansas, Texas, and California. Some of the experiments have now been continued for five years.

The results may be briefly summarized. The original pure type of Kubanka wheat from South Dakota showed entirely different morphological characteristics and chemical composition at the different stations. The characteristics of the wheats of one variety at any particular station were uniform for the wheat whenever grown at that station, no matter from which station the seed had been derived. Thus, when South Dakota wheat was grown in Kansas or California, it assumed characteristics different from those which it originally had, and peculiar for each region; but if, after several generations, these wheats were again transferred to South Dakota the resulting crop assumed all the characteristics of the same variety grown continuously in South Dakota. The series with Crimean wheat gave exactly similar results.

The experiments show that wheats of one variety from several sources, when grown in the same locality, differ but little in morphological characteristics and chemical composition, but if grown in different localities from seed of the same source, they differ widely from each other. There is a marked response to environment, but all the plants of a pure variety respond in the same way. There is no tendency toward "breaking up" of the type on account of change in environment.—H. HASSELBRING.

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[5] LE CLERC, J. A., and LEAVITT, S., Tri-local experiments on the influence of environment on the composition of wheat. U.S. Dept. Agr., Bur. Chem., Bull. 128. pp. 18. 1910.

Alcoholic fermentation.—KOHL[6] has carried on a study of the series of reactions involved in alcoholic fermentation. He finds that lactic acid is not fermented either by zymase, compressed yeast, or bottom yeast; that 1 per cent or more of lactic acid stops the self-fermentation of living yeast and strongly reduces its fermentative activity in glucose; but that zymase, compressed yeast, and brewer's yeast ferment sodium lactate speedily. It is evident that if at one stage of alcoholic fermentation lactic acid is found, it must exist as a salt. The fact that zymase will not ferment lactic acid has been urged against BUCHNER'S conception that alcoholic fermentation takes place in two steps; glucose is transformed to lactic acid by zymase, and lactic acid to alcohol and carbon dioxid by lacticidase. KOHL'S finding answers this argument. While he thinks the fermentation occurs in these two steps, he differs in his view of the enzymes that carry on the processes. He concludes that catalase transforms the glucose to lactic acid, and that zymase carries the splitting on to alcohol and carbon dioxid. In a glycerin extract of crushed yeast, he found neither an oxidase nor a peroxidase, as shown by an alcoholic solution of quaiac; yet it contained an enzyme capable of oxidizing various phenols, and these oxidations he believes are carried on by the catalase present. This extract when filtered produces lactic acid in the presence of glucose—it likewise produces a trace of oxalic acid. He does not know whether both these oxidations are due to the same enzyme. He urges that this view locates the function of the catalase of yeast, a point not before settled. In case zymase is present, the oxidations go no farther than lactic acid, which is then transformed to alcohol and carbon dioxid. In its absence, the oxidation is carried still farther, producing various other acids. He applies his view to the explanation of the results of HARDEN and YOUNG with the gelatin filter, but cannot be said in any degree to further elucidate them. This subject, because of its close bearing on respiration and energy-production in the organism, certainly needs much attention from biological chemists. It is disappointing, however, that the contributions are mainly hypotheses with sparse experimental evidence, rather than records of careful chemical studies.—WILLIAM CROCKER.

Adoxa moschatellina.—The uncertain systematic position of *Adoxa* induced LAGERBERG[7] to undertake a complete morphological and cytological investigation of this peculiar genus. The development of the various organs was traced, and this comparatively simple part of the study is illustrated by figures in the text; while the cytological details of spermatogenesis, oogenesis, and fertilization are illustrated by three large plates. The following are some of the principal features: The ovule has a single integument and a single archesporial cell which

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[6] KOHL, F. G., Ueber das Wesen der Alkoholgärung. Beih. Bot. Centralbl. **29**[1]:115–126. 1910.

[7] LAGERBERG, T., Studien über die Entwickelungsgeschichte und systematische Stellung von *Adoxa moschatellina*. Kungl. Sv. Vet. Akad. Handl. **44**:1–86. *pls. 1–3. figs. 23.* 1909.

develops directly into the embryo sac, as in *Lilium*, the four megaspores, not separated by walls, all taking part in the formation of the sac. The two male cells retain their form even after passing to the end of the pollen tube. Double fertilization was observed. The diploid and haploid chromosome numbers are 38 and 18. The first four cells of the endosperm are long and tubelike, extending from the egg to the antipodals.

Various genera of the Saxifragaceae, Araliaceae, Caprifoliaceae, and Ranunculaceae, with which various systematists have supposed *Adoxa* to be related, were studied for comparison, and one of these genera (*Sambucus*) shows so many resemblances that the similarity could hardly be accidental. For instance, both have ovules with a single integument and a single archesporial cell which develops into the embryo sac according to the *Lilium* type; the wall of the anther, the cytological details of the development of the pollen (including the number of chromosomes), and the structure of the mature pollen grain are so identical that the two forms can hardly be distinguished in these respects; the long persistence of the organized male cells is the same in both, and resemblances in the grosser morphology were already well known. The conclusion is reached, and it seems to be based upon an unusually wide range of evidence, that there is no need for the family Adoxaceae, and that *Adoxa* should be placed in the Caprifoliaceae in the tribe Sambuceae.—CHARLES J. CHAMBERLAIN.

Geotropism.—Under a very pretentious title, GILTAY[8] discusses and describes a number of experiments on some of the "fundamental questions of geotropism." The article is more a contribution to the teaching of the subject than to knowledge. He gives an excellent method for lecture demonstration of the force with which a geotropically bending primary root turns downward. He also points out that we have never proved that gravity is the only stimulus involved in the turning of the primary root toward the center of the earth. The only evidence we have for this is qualitative. KNIGHT showed (1806) that as the centrifugal force was increased on a centrifuge with a vertical axis the root and stem took more nearly the horizontal position; but he did not show any relation between the position of the stem and root and the resultant of the two forces which he assumed to be involved (gravity and centrifugal force). In short, KNIGHT showed that at least in part the so-called geotropic stimulus is the gravity stimulus, but he did not show that the gravity stimulus is the only stimulus involved. GILTAY urges the necessity of showing that the position taken by orthotropic organs on such a centrifuge is the resultant of the two forces, if we are to be assured that the geotropic stimulus is identical in nature with the gravity stimulus and with the stimulus of centrifugal force. The resultant of the two forces ought of course to be the position taken, provided the two forces do not differ from each other by many fold, for we must remember that WEBER'S

[8] GILTAY, E., Einige Betrachtungen und Versuche über Grundfragen beim Geotropismus der Wurzel. Zeitschr. Botanik **2**:305–331. 1910.

law applies in geotropism as in various tropic responses. GILTAY devised a special centrifuge with a vertical axis for testing this point. He finds that with the average of 368 tests, with the angle of the resultant approximating 45°, the primary root fell 2.1° below the resultant. This deviation can well be accounted for by the variation in speed of rotation and the variation of roots themselves. This seems to furnish evidence for the identity in nature of the geotropic and centrifugal stimuli.—WILLIAM CROCKER.

Rôle of hydrocyanic acid.—TREUB[9] has found that the amount of hydrocyanic acid in plants of *Sorghum* increases during the day, not due to the direct action of light, but in proportion to the formation of the products of the assimilation of carbon. It was already known, from investigations with *Pangium edule* and *Phaseolus lunatus*, that light has no part in the formation of hydrocyanic acid except as it favors photosynthesis. Much the same results have been obtained with *Prunus javanica*. *Passiflora foetida* and at least four other plants offer examples for the demonstration of the direct proportion between the formation of hydrocyanic acid and the function of chlorophyll. This can be demonstrated also by the use of variegated leaves. The amount of acid is usually greatest in the young leaves and gradually diminishes as the leaves grow older. With *Sorghum*, young leaves grown in a dry season or on dry soil contain much acid, and for this reason are dangerous as food for stock. Leaves about to fall contain very little acid, while, with only two exceptions, those already fallen contain none. GUIGNARD found that fallen leaves of *Sambucus nigra* contain much of the acid. TREUB confirms these results and finds the same to be true of fallen leaves of *Indigofera galegoides*. The hydrocyanic acid is probably the first recognizable simple organic product of the assimilation of nitrogen, and perhaps the first organic nitrogen compound formed. The amounts of the acid in plants watered with a solution of sodium and potassium nitrate increased or decreased in proportion to the amount of nitrate used. RAVENNA and PELI think that nitrates and carbohydrates are necessary to the formation of the acid. TREUB agrees with these conclusions, and adds that dextrose is especially essential. The acid probably does not occur in plants as such, but in the form of a glucoside from which it can be liberated by an enzyme or by boiling water.—R. CATLIN ROSE.

Parasitic flagellates in plants.—Although rapid progress in the study of parasitic flagellates has shown them to be of widespread occurrence in animal organisms, the discovery of these parasites in plants is a noteworthy fact. The occurrence of a trypanosome-like parasite in the latex of *Euphorbia pilulifera* in Mauritius was first reported by LAFONT.[10] The discovery was soon afterward

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[9] TREUB, M., Nouvelles recherches sur le rôle de l'acide cyanhydrique dans les plantes vertes. Ann. Jard. Bot. Buitenzorg II. **8**:84–118. 1910.

[10] LAFONT, A., Sur la présence d'un parasite de la classe des Flagellés dans le latex de *l'Euphorbia pilulifera*. Compt. Rend. Soc. Biol. **66**:1011–1013. 1909.

confirmed by DONOVAN[11] by observations on the same species of Euphorbia in Madras. LAFONT[12] now follows with a full account of the organism. The parasite, which was originally discovered in the latex of *Euphorbia pilulifera*, occurs also in the two other species *E. thymifolia* and *E. hypericifolia*. A search of the latex of some 50 other species of plants from various families failed to reveal similar organisms. About one-third of the *Euphorbia* plants from different stations were found to be infected. The number of parasites in different plants varies greatly. The infected plants show the effects of malnutrition, and finally drop their leaves and die. The protozoans are elongated, flattened, and somewhat undulate. They do not, however, possess the undulating membrane of trypanosomes, and are therefore placed in the genus *Leptomonas*, as *L. Davidi*. The apex is provided with one cilium, which originates in a blepharoplast. A large nucleus is situated near the center of the body. Division, which was observed in hanging drop cultures, takes place by longitudinal fission, preceded by a thickening of the body of the organism. Various forms, perhaps indicating different stages in the development of the organism, were observed. The simplest are spherical, nucleated masses of protoplasm, which soon form a cilium. It is possible that two parasites exist here. Injection of the parasites into the blood of small animals produced no infection, although some of the animals died from unknown causes.—H. HASSELBRING.

Diseases of celery.—KLEBAHN[13] has added to his numerous excellent contributions of life histories of *Fungi imperfecti* an account of two diseases of celery occurring in the truck gardens on the lowlands surrounding Hamburg. The first is the leaf-spot disease caused by *Septoria Apii* (Briosi and Cav.) Rostr., also known as *S. Petroselini* Desm. var. *Apii*, and as *Phlyctaena Magnusiana* (Allechr.) Bres. The fungus attacks the leaves, stems, and fruits of the celery plants, and forms pycnidia on all of these organs. In following out the manner in which the fungus lives through the winter, the author encountered no other fruiting stages. The fungus is carried over from year to year by means of spores which persist both in the pycnidia on the plant remnants left in the fields, and in the pycnidia on the seeds. With spores from both sources the author was able to produce infections on young plants with ease.

The second disease is a scab of the roots, which, although it has been reported from several places, has never been critically studied. The disease is shown to be due to a species of *Phoma*, for which the author here first uses the name *Ph. apiicola*, unfortunately without giving a technical description of the fungus.

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[11] DONOVAN, C., Kala-azar in Madras, especially with regard to its connection with the dog and the bug (*Conarrhinus*). Lancet **177**:1495–1496. 1909.

[12] LAFONT, A., Sur le présence d'un *Leptomonas*, parasite de la classe des Flagellés dans le latex de trois Euphorbiacées. Ann. Inst. Pasteur **24**:205–219. *figs.* 7. 1910.

[13] KLEBAHN, H., Die Krankheiten des Selleries. Zeitschr. Pflanzenkrank. **20**: 1–40. *pls.* 2. *figs.* 14. 1910.

The pycnidia occur on the diseased roots, and more abundantly on the lower part of the petioles and on the fruit, but rarely on the leaves. Cultures were obtained from hyphae invading the sound tissue of the roots and from spores. The colonies from both sources were similar, and many infection experiments with mycelium from both sources on sound roots were successful. The action of this species of *Phoma* in producing a scab and rotting of celery tubers is a case analogous to the well-known root rot of sugar beets caused by another species of the same genus, *Ph. Betae*.—H. HASSELBRING.

Treatment for smuts.—The usual methods of treating seed-grain for the prevention of smuts have not proved applicable in the case of the loose smuts of wheat and barley, since these fungi persist through the winter, not by means of spores adhering to the surface of the grain, but by means of a dormant mycelium in the interior of the seed. APPEL,[14] following out the suggestion made by JENSEN at the time of the publication of his hot water treatment to use a preliminary treatment with cold water for seed infected with these smuts, has worked out a more definite method founded on an experimental basis. APPEL assumes that, like the spores of smuts, the dormant mycelium will start into growth more readily than the infected seed, and that the active mycelium will be killed at temperatures which do not injure the seed. The experiments substantiate this belief. It is found that grain infected with *Ustilago tritici* or *U. nuda* can be treated successfully by being soaked for six hours at 20–30° C., and by being treated subsequently with hot water at 50–54° C., or by hot air at a corresponding temperature.—H. HASSELBRING.

Dehiscence of anthers.—HANNIG [15] takes up what apparently he regards as a real difference between STEINBRINCK'S cohesion theory and SCHNEIDER'S *Schrumpfungstheorie* for the explanation of the dehiscence of anthers. To the reviewer the two theories differ more in the degree of analysis than anything else, as he believes that this phenomenon must be in the last analysis found dependent upon the tensile strength of water. However, the author has done a real service in showing how the dehiscence is a genuine cohesion consequence. He has accomplished this by artificially causing dehiscence through the effect of dehydrating solutions. He has shown that dehiscence will occur in a saturated atmosphere if anthers are exposed to light which generates enough heat in the tissues to reduce the vapor tension sufficiently to set up tension in the water contained in the membranes. BURCK'S notion that the nectaries withdraw water from the membranes and hence cause dehiscence in a saturated atmosphere was not confirmed.—RAYMOND H. POND.

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[14] APPEL, OTTO, Theorie und Praxis der Bekämpfung von *Ustilago tritici* und *Ustilago nuda*. Ber. Deutsch. Bot. Gesell. **27**:606–610. 1910.

[15] HANNIG, E., Ueber den Offnungsmechanismus der Antheren. Jahrb. Wiss. Bot. **47**:186–218. 1909.

Plant diseases.—WHETZEL and STEWART,[16] contrary to the common belief, advocate the cultivation of pear orchards if a crop of fruit is desired. In this view they are upheld by HEDRICK of the State Station, who found that blight epidemics are not necessarily dependent upon cultivation and manuring. No immunity to the disease was obtained by the use of certain blight remedies.

SACKETT[17] has described the appearance of this new bacterial disease in the field, and has given the manner of infection, together with a complete morphological, cultural, physical, and biochemical description of the causal organism, *Pseudomonas medicaginis* sp. n. The work is well supported by numerous inoculations. The only thing lacking in this well-balanced investigation is a bibliography.—VENUS W. POOL.

Source of nitrogen for molds.—RITTER[18] finds that the ammonium salts of mineral acids as the source of nitrogen for the molds is inverse to the strength of the acid forming the negative ion of the salt. The author attributes this to the toxic effect of the acid liberated by the assimilation of the ammonium ion. For instance, mono-ammonium or diammonium phosphate is a far better source of nitrogen than the ammonium salts of sulfuric, hydrochloric, or nitric acids. The so-called "Nitratpilze" (*Aspergillus glaucus*, *Mucor racemosus*, *Cladosporium herbarium*) gave on the average a greater yield of organic material from the two ammonium phosphates mentioned than from potassium nitrate. The yield from the ammonium salts of the stronger mineral acids was very much lower.—WILLIAM CROCKER.

Excretion of salts by Statice.—SCHTSCHERBACK[19] has investigated the excretion of salts by the leaves of *Statice Gmelini*. Many leaves of halophytes are known to excrete salts in considerable quantities by means of the glands described by DEBARY and others. Leaves of *Statice Gmelini*, floating on pure water, are soon freed from their contained salt and thereafter excrete water only. The amount of excretion of a leaf floating on a solution of a substance depends upon the substance and the concentration of it used; sulfates and chlorids of sodium, potassium, and magnesium tending to increase it, while calcium compounds and sugars decrease it. The amount of excretion does not depend upon the turgor pressure in the leaf cells.—R. CATLIN ROSE.

Physcia villosa in North America.—In a recent number of this journal (**49**: 320. 1910) I recorded this plant from southern California. Since then I have

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[16] WHETZEL, H. H., and STEWART, V. B., Fire blight of pears, apples, quinces, etc. Bull. N.Y. Cornell Exp. Sta. **272**:31–51. *figs. 5–231*. 1910.

[17] SACKETT, W. G., A bacterial disease of alfalfa. Bull. Colo. Exp. Sta. **158**:1–32. *pls. 1–3*. 1910.

[18] RITTER, G., Ammoniak und Nitrate als Stickstoffquelle für Schimmelpilze. Ber. Deutsch. Bot. Gesell. **27**:582–588. 1909.

[19] SCHTSCHERBACK, JOHANN, Ueber die Salzausscheidung durch die Blätter von *Statice Gmelini*. Beih. Deutsch. Bot. Gesell. **28**:30–34. 1910.

found in the herbarium of Wellesley College a specimen distributed with *Evernia furfacea* (L.) Mann, collected by EDWARD PALMER at San Diego, California, in December 1888. A duplicate of this collecting has been kindly sent me by Dr. L. W. RIDDLE, who also calls my attention to the fact that this plant was distributed in *Decades North American Lichens* (no. 154) from San Quintin Bay, Lower California, Mexico, where it was collected by C. R. ORCUTT (see HASSE, Bryologist **13**:61. 1910).—R. HEBER HOWE, JR., *Thoreau Museum, Concord, Mass.*

Fertilization in Rafflesia.—The remarkable and renowned *Rafflesia* has long attracted attention, but little has been known of its more minute details. An investigation[20] of its embryo sac and fertilization shows that in spite of the parasitic habit and grotesque appearance, the development of the embryo sac and the process of fertilization are quite normal. It was noted that young stages in the development of the ovule are found in nearly mature buds, and that the development of the sac takes place after the flower is open.—CHARLES J. CHAMBERLAIN.

Microchemistry of chromosomes.[21]—The title arouses interest, but from the paper we learn only that chromosomes may be dissolved in hot water, while the reticulum of the resting nucleus is little affected, and that therefore the importance of chromatin in heredity has been overestimated. That there are chemical changes as chromosomes are developed from a reticulum has been known for some time, but we now know the effect of hot water upon chromosomes and theories of heredity.—CHARLES J. CHAMBERLAIN.

Absorption of salts by Bromeliaceae.—From his work with the Bromeliaceae, Aso[22] concludes that *Ananas sativus*, *Pitcairnia imbricata*, and *Nidularia purpurea* do not take up, or only in very small amounts, by means of the scales of the leaves, salts soluble in water. On the other hand, *Tillandsia usneoides*, after five days of submergence in a 0.3 per cent lithium nitrate solution, showed in different parts of the plant considerable quantities of the salt.—R. CATLIN ROSE.

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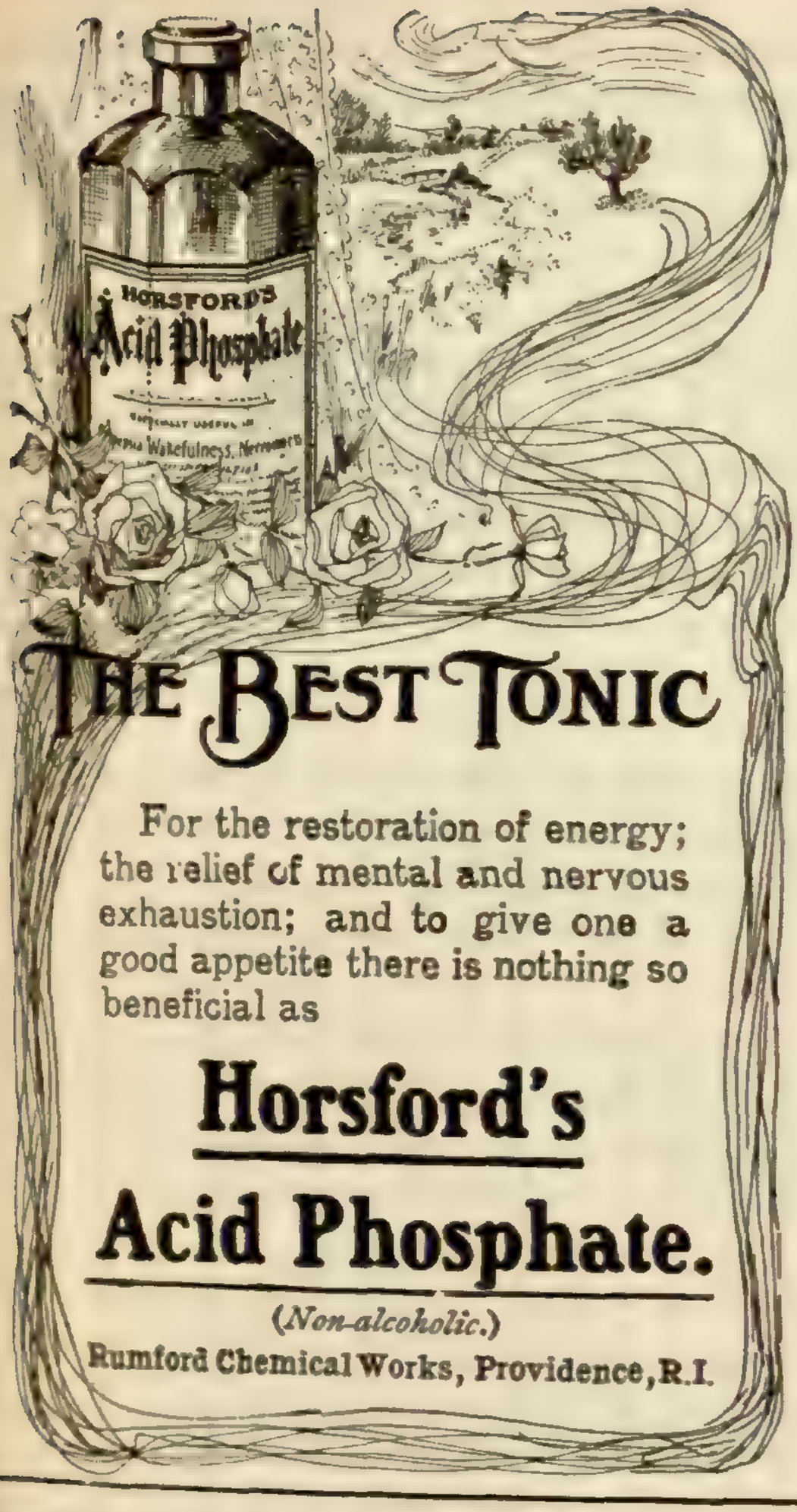
[20] ERNST, A., und SCHMID, ED., Embryosack entwickelung bei *Rafflesia Patma* Bl. Ber. Deutsch. Bot. Gesell. **27**:176–186. *pl. 8*. 1909.

[21] NĚMEC, B., Zur Mikrochemie der Chromosomen. Ber. Deutsch. Bot. Gesell. **27**:43–47. 1909.

[22] ASO, K., Können Bromeliaceen durch die Schuppen der Blätter Salze aufnehmen? Flora **100**:447–449. 1910.



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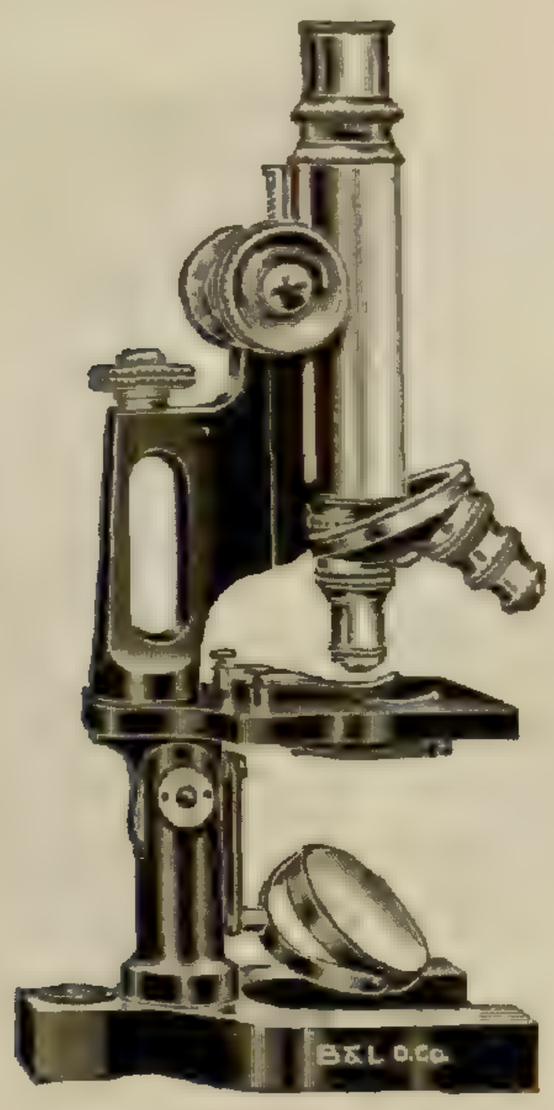

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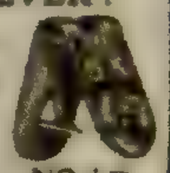

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VOLUME L NUMBER 3

BOTANICAL GAZETTE

SEPTEMBER 1910

SOME EFFECTS OF A HARMFUL ORGANIC SOIL CONSTITUENT[1]

OSWALD SCHREINER AND J. J. SKINNER

(WITH ELEVEN FIGURES)

The investigation of infertile soils from various parts of the United States has received considerable attention in the last few years, and has been conducted along several converging lines in these laboratories. Among these is a thorough inquiry into the nature of the organic matter of soils. The results of these researches into the chemistry of the organic matter of the soil, its origin, transformation, and properties, have been reported upon to a large extent in a former bulletin of this Bureau and in scientific journals.[2] Several bodies have been isolated from such soils, which have quite different chemical properties, thus showing that there

[1] Published by permission of the Secretary of Agriculture.

[2] SCHREINER, O., and SHOREY, E. C., The isolation of dihydroxystearic acid from soils. Jour. Amer. Chem. Soc. **30**:1599. 1908.

———, The isolation of picoline carboxylic acid from soils and its relation to soil fertility. Jour. Amer. Chem. Soc. **30**:1295. 1908.

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———, The presence of secondary decomposition products of proteids in soils. Proc. Amer. Soc. Biol. Chem. **1**:47. 1907.

See also Bull. 53, Bureau of Soils, U.S. Dept. Agric.

SCHREINER, O., and SULLIVAN, M. X., Soil fatigue caused by organic compounds. Jour. Biol. Chem. **6**:39. 1909.

is a difference in the nature of the chemical bodies in different soils. Some of the bodies isolated contained nitrogen, while others free from this element contained carbon, hydrogen, and oxygen only. The presence of sulfur and phosphorus compounds has also been strongly indicated by these studies, although the actual identification of bodies of such nature has not been definitely accomplished. The results are sufficient, however, to show that a wide range of bodies of different composition exists in soils, and a more detailed knowledge of their nature and properties seems imperative in order to know and understand the nature of the material influencing crops in the field and the action of fertilizers upon these, either directly or indirectly, through the medium of root oxidation and reduction or by microbiologic and enzymotic influences.

In an earlier paper[3] it was demonstrated that the roots of plants possessed a very appreciable oxidizing power. This oxidizing power of the normal root was found to be influenced by the medium in which it grew. Thus good soils and their aqueous extracts promoted oxidation, while the poorer soils hindered this function of the roots. Some substances harmful to plant growth were also found to have an inhibitive effect on this oxidation. When smaller amounts were present, however, it was found that the oxidizing power of the roots was able to overcome the harmful influence. An examination in one case, namely that of vanillin, where it was possible to demonstrate by colorimetric test the presence or absence of minute amounts, showed that this disappeared entirely from solution under the influence of the oxidizing power of the roots. It was further shown that the fertilizer salts, in addition to promoting plant growth, also had a very strong influence in promoting this enzymotic effect, this being especially marked in the case of sodium nitrate and lime.[4] The action of fertilizer salts and the influence of such harmful soil constituents were further investigated, therefore, and the results given in connection with the

[3] SCHREINER, O., and REED, H. S., Studies on the oxidizing power of roots. BOT. GAZETTE **47**:355. 1909. See also Bull. 56, Bureau of Soils, U. S. Dept. Agric. 1909.

[4] SCHREINER, O., and REED, H. S., The power of sodium nitrate and calcium carbonate to decrease toxicity in conjunction with plants growing in solution cultures Jour. Amer. Chem. Soc. **30**:85. 1908.

other factors reported in this paper. All of the harmful bodies which had been studied and presented in previous papers had a distinct influence on the roots, causing them in many cases to become stunted or swollen and darkened at the tips, or to show other physiological irregularities of the same kind as is exhibited by the roots in different extracts from infertile soils. It is, therefore, of interest to know further the influence which such altered root conditions would have upon the composition of the soil solution and the influence of added fertilizers.

One of the bodies isolated from a number of unproductive soils is a definite crystalline body identified as dihydroxystearic acid melting at 98°–99° C. It can be prepared by the oxidation of elaidic acid in the laboratory. In these experiments the dihydroxystearic acid used had been prepared in this manner. The frequent occurrence of this body in such soils and its disappearance therefrom by processes which promote aeration or oxidation made this especially suitable for further study of its effects on plant development in relation to the concentrations of soil solutions or fertilizer application.

The dihydroxystearic acid can be isolated from a soil containing it by treatment with a 2 per cent sodium hydroxid solution, and, after allowing the mineral material to settle, the alkaline extract is separated and made acid with a slight excess of acetic acid. The so-called humus precipitate which is thus formed is filtered off and the clear filtrate is shaken out with ether and the ether solution allowed to evaporate on the surface of a small quantity of water. The dihydroxystearic acid is left on the surface of the water, together with other impurities extracted by the ether. The impurities can be largely removed by heating the water to boiling, and filtering. Fig. 1 shows the effect of a solution of this nature on wheat seedlings when the material is dissolved in much water. The dihydroxystearic acid, when dissolved in a small volume of water and then cooled, crystallizes out in the form of small plates or leaflets arranged in radiating clusters. Fig. 2 shows the effect of the purified substance in various concentrations. The details of the method of isolating and purifying will be found in the paper cited.

Dihydroxystearic acid can also be prepared in the laboratory by starting with oleic acid, which by treatment with nitrous oxid is changed to the isomeric elaidic acid. The elaidic acid thus formed is dissolved in a solution of potassium hydroxid and oxidized by a solution of potassium permanganate, one of the products under suitable conditions being dihydroxystearic acid.

FIG. 1.—Wheat seedlings grown in extract obtained in the method for isolating dihydroxystearic acid from soils: *1*, *2*, undiluted extract; *3*, *4*, one part of extract, one part of distilled water; *5*, *6*, one part of extract, nine parts of distilled water.

Care has to be taken that the oxidation does not proceed too far, for the dihydroxystearic acid, as already mentioned above, is very readily oxidized to other compounds.

In this paper are reported experiments on the effect of a harmful soil constituent upon plant growth and upon soil solutions and fertilizer action, especially with reference to the ratio of phosphate, nitrate, and potash originally present and removed by wheat seedlings in the course of the experiment.

Solution cultures containing the three fertilizer ingredients, namely P_2O_5, NH_3, and K_2O, as calcium acid phosphate, sodium nitrate, and potassium sulfate, respectively, in all possible ratios of one, two, and three constituents, varying them in stages of 10 per cent, were prepared, the concentration being 80 parts per million in these constituents. In a similar set of cultures there

FIG. 2.—Wheat seedlings grown in solutions of dihydroxystearic acid from soils: *1*, solution of dihydroxystearic acid, 200 parts per million; *2*, 100 parts; *3*, 50 parts; *4*, 20 parts; *5*, control in distilled water.

was added 50 parts per million of dihydroxystearic acid to each culture. The selection of the salts as carriers of the phosphate, nitrate, and potash, and the terms P_2O_5, NH_3, and K_2O are in harmony with the practice in fertilizer work. The salts selected, it will be seen, are also carriers of calcium, of sodium, and of sulfate, and the three salts, therefore, were practically the best that could be selected for giving at the same time other needed constituents. The details of this method of experimentation have been given in

an earlier paper, and the reader is referred to this for a full explanation of the use of the triangular diagram and the results obtained by growing seedling wheat in these various culture solutions without the presence of any added harmful substance.[5] Wheat seedlings were then grown in these various cultures and observations made in regard to general development, the effect on the root growth and appearance, and on root oxidation, and at the termination of the experiment the green weight of the plants was taken. The solutions were changed every three days and an analysis made, the phosphate, nitrate, and potash being determined, thus giving the concentration of these elements and their ratios existing at the end of every three-day period for comparison with the original concentration and ratio. This changing of the solutions was kept up for twenty-four days, thus making eight changes.

In the present work a triangle of solution cultures similar to the one described in the previous paper was set up, with the difference that 50 parts per million of dihydroxystearic acid were present in each culture. This set of cultures grew from April 2 to April 26. The set without the dihydroxystearic acid grew from February 26 to March 21. While these two sets are not strictly comparable, owing to the fact that they were grown at different times, though under very similar greenhouse conditions and for the same length of time as well as in the same time of year, one closely following the other, the results show, nevertheless, very strikingly the effect of dihydroxystearic acid, and are duplicated or substantiated by two further experiments in which the sets were grown simultaneously.

The analytical results, however, were not so complete in these later tests, owing to the inability to handle the 396 separate determinations necessary every three days. The results given in this paper, therefore, are largely based on the first set, for the reason that the analytical results were more complete than in the other sets mentioned.

The difference between the cultures containing the dihydroxystearic acid and those without this substance was very marked,

[5] SCHREINER, O., and SKINNER, J. J., Ratio of phosphate, nitrate, and potassium on absorption and growth. BOT. GAZETTE 50:1. 1910.

and was especially striking in those sets where both triangles of cultures were grown simultaneously. In addition to the general appearance of the tops, the presence of this harmful body produces still other effects readily recognized by the investigator, and forming on the whole a better physiological indicator of the toxicity than the growth of tops, as has been well recognized by physiologists generally in conducting similar work. Reference is here made to the action of the body on root condition and growth. The root being bathed by the solution, and being, moreover, the delicate mechanism of absorption, is often a more sensitive indicator than is the growth of the top. The most marked effects of dihydroxystearic acid on roots are strongly to inhibit their growth and to produce enlarged or swollen tips, which are frequently very dark in color and often turned back in the form of hooks. These phenomena are observed even when the injury is not so great as to kill the plants. This action of the body on the roots is influenced by the conditions of growth imposed upon the plant by the different fertilizer ratios. This is shown by the general notes taken on one of these sets one week after growth in the cultures had begun.

All the plants in the solutions having no nitrogen appear to be dying. The roots are already dead, have made little growth, and are much discolored, the tips are dark and swollen and a large number turned upward. The tops have made some growth, some of the leaves are curled, but most are still fresh and green.

The plants in the solutions containing no phosphate are similar to the above; the roots and tops are somewhat better, but still show an undoubted harmful action, the roots being dark and flimsy, tips swollen and often turned upward, the greater number being dead.

The plants in the solutions on the potash base line are better than the two sets described above. The upper parts of the roots of these plants are dark, the lower sections that have recently grown out are white and clear, but the tips are still dark and swollen, and many are turned upward.

The plants in the interior of the triangle, where all three fertilizer ingredients are present, are fairly good, with no great difference noticeable at this stage, but showing somewhat better plants near

the center. The roots, on the other hand, are already showing differences. They are rather poor along the line having 8 parts per million of NH_3. The upper and older part of the roots is dark, the newer portion is white and clear, but the tips are swollen. The general condition of the roots, as a whole, is a great deal better than in case of those in the boundary lines of the triangle. The condition of the roots on the line having 8 parts per million P_2O_5, and on the line having 8 parts per million K_2O, are about the same as on the 8 parts per million NH_3 line.

Farther within the triangle the general condition of the roots is much better. The solutions in cultures number 25, 32, 33, 34, 42, and 43 show by their roots that the harmful effect of the substance has been somewhat overcome: they are lighter than the others, in fact most of the roots, except the upper and older sections, are white and clear, but the tips are still slightly swollen and somewhat bent.

Another property of the roots which is influenced by harmful bodies is that of root oxidation. It has been shown that plant roots possess a very appreciable power of oxidation, and that this power is stronger in good soils than in poor, or in their extracts, and that harmful bodies retard this oxidation, and beneficial bodies augment it. Fertilizer salts were shown to increase root oxidation, and through this action a reduction in the quantity of the harmful body present was produced.

Some further observations were made in connection with the present investigation in regard to oxidation and the effect of dihydroxystearic acid upon this function. The effect was so marked in the concentrations used, namely 50 parts per million, that the roots at the end of the experiment were found to be almost wholly lacking in ability to oxidize aloin used as an indicator in the manner described in the publication referred to above. Some oxidizing power was still possessed by the cultures in the interior of the triangle, where, as mentioned above, the growth was better than in other regions, although even here the power of oxidation was greatly impaired. Nevertheless, it is interesting to note that the condition which produced the best general development of the plants is closely associated with a power of root oxidation.

FIG. 3.—Wheat plants growing in a culture solution containing a fertilizer mixture composed of phosphate 60 per cent, nitrogen 20 per cent, potash 20 per cent: *1*, without dihydroxystearic acid; *2*, with dihydroxystearic acid.

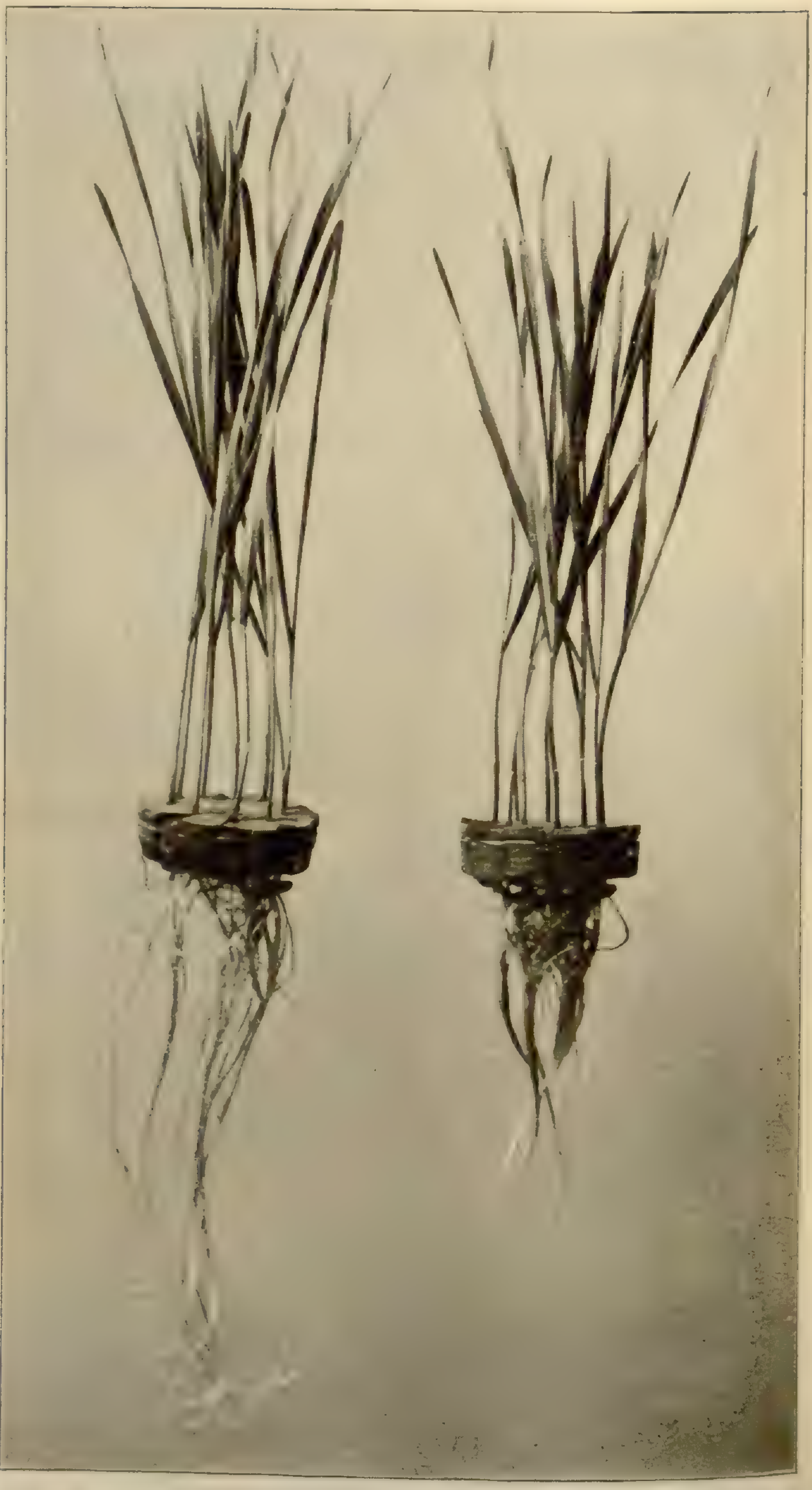

FIG. 4.—Wheat plants growing in a culture solution containing a fertilizer mixture composed of phosphate 20 per cent, nitrogen 60 per cent, potash 20 per cent: *1*, without dihydroxystearic acid; *2*, with dihydroxystearic acid.

Lower concentrations of dihydroxystearic acid would doubtless be better suited for a more thorough study of this matter.

Some of the plants grown in solutions with and without dihydroxystearic acid are shown in figs. 3, 4, and 5. The cultures taken represent a fertilizer rich in phosphoric acid, one rich in nitrate, and one rich in potash. The results shown in these photographs are representative of the general effect over all the region of the triangle from which they are taken.

GREEN WEIGHT OBTAINED IN THE VARIOUS CULTURES

The green weights obtained in the 66 cultures of the first set are given in the triangular diagram shown in fig. 6. It will be seen that, in harmony with the results given in the previous paper reporting the experiment without the harmful substance, the growth with the single elements or along the lines where mixtures of two occurred was in general less than within the triangle. The region of greatest growth in the solutions without the dihydroxystearic acid was approximately in the middle of the 10 and 20 per cent phosphate lines. In the dihydroxystearic acid cultures it might be said in general that this region of greater growth was displaced along these lines toward the nitrogen side.

The total growth made in the 66 cultures without the dihydroxystearic acid was 207 grams as against 114 grams in the case of the 66 cultures with the 50 parts per million of dihydroxystearic acid, or, putting the first as 100, the latter becomes 55. In other words, the plants with the dihydroxystearic acid made only, as an average of the 66 cultures, a growth of 55 per cent. It will be seen that the harmful substance produced its greatest effect in general along the periphery of the triangle, except, perhaps, along the phosphate-nitrogen line. In the interior of the triangle, where the greater growth occurred under the more normal conditions, the depression caused by the substance was not so marked, and this seems to be especially true in the region nearer to the nitrate end, in which, as already pointed out, the greater growth occurred in the cultures where the dihydroxystearic acid was present.

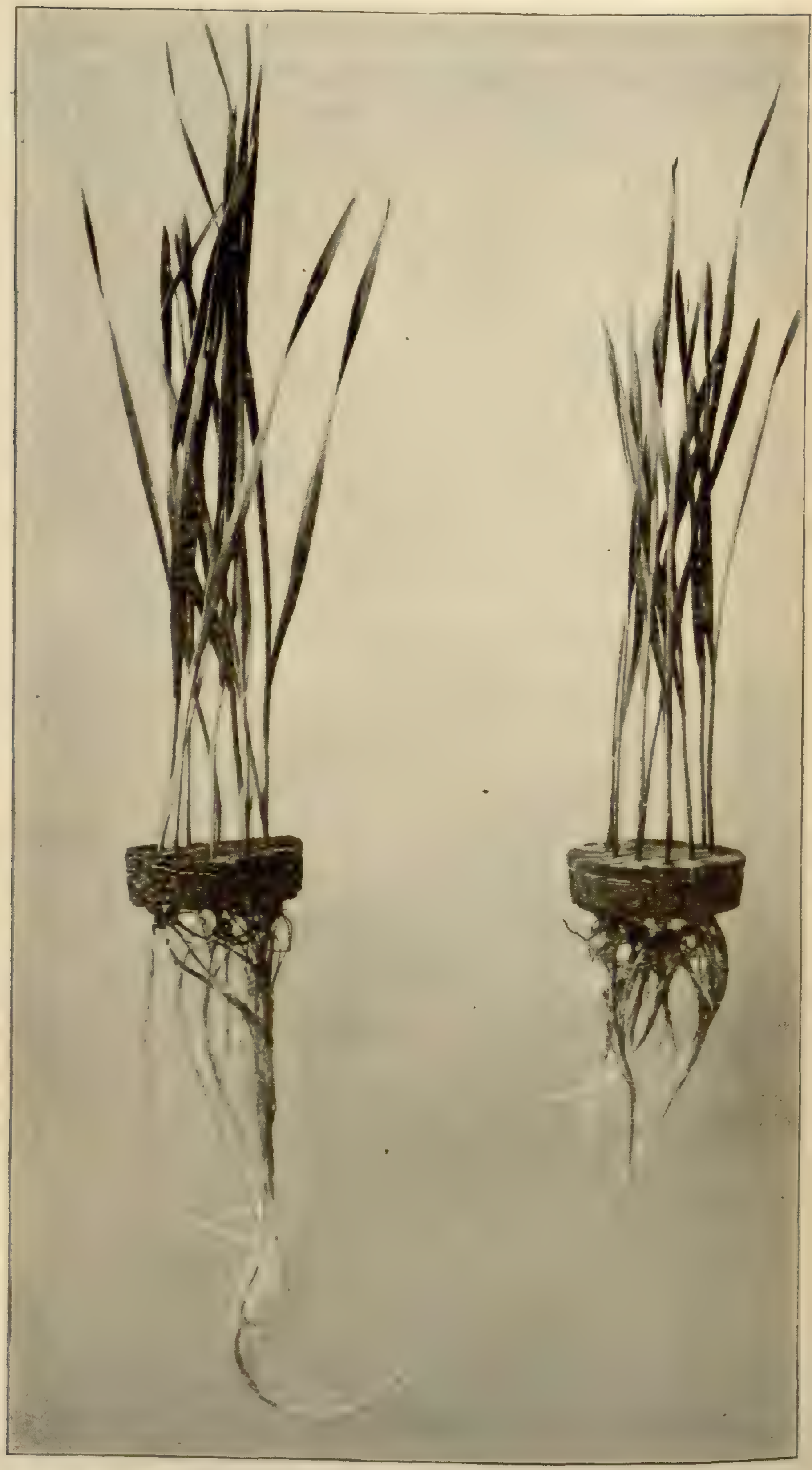

FIG. 5.—Wheat plants growing in a culture solution containing a fertilizer mixture composed of phosphate 20 per cent, nitrogen 20 per cent, potash 60 per cent: *1*, without dihydroxystearic acid; *2*, with dihydroxystearic acid.

CONCENTRATIONS OF $P_2O_5 + NH_3 + K_2O$ FOUND IN THE VARIOUS CULTURES

As has already been stated, the solutions were analyzed every third day for the three component fertilizer parts, phosphate, nitrate, and potassium, expressed as P_2O_5, NH_3, and K_2O. The original concentration in these elements was in the sum total 80

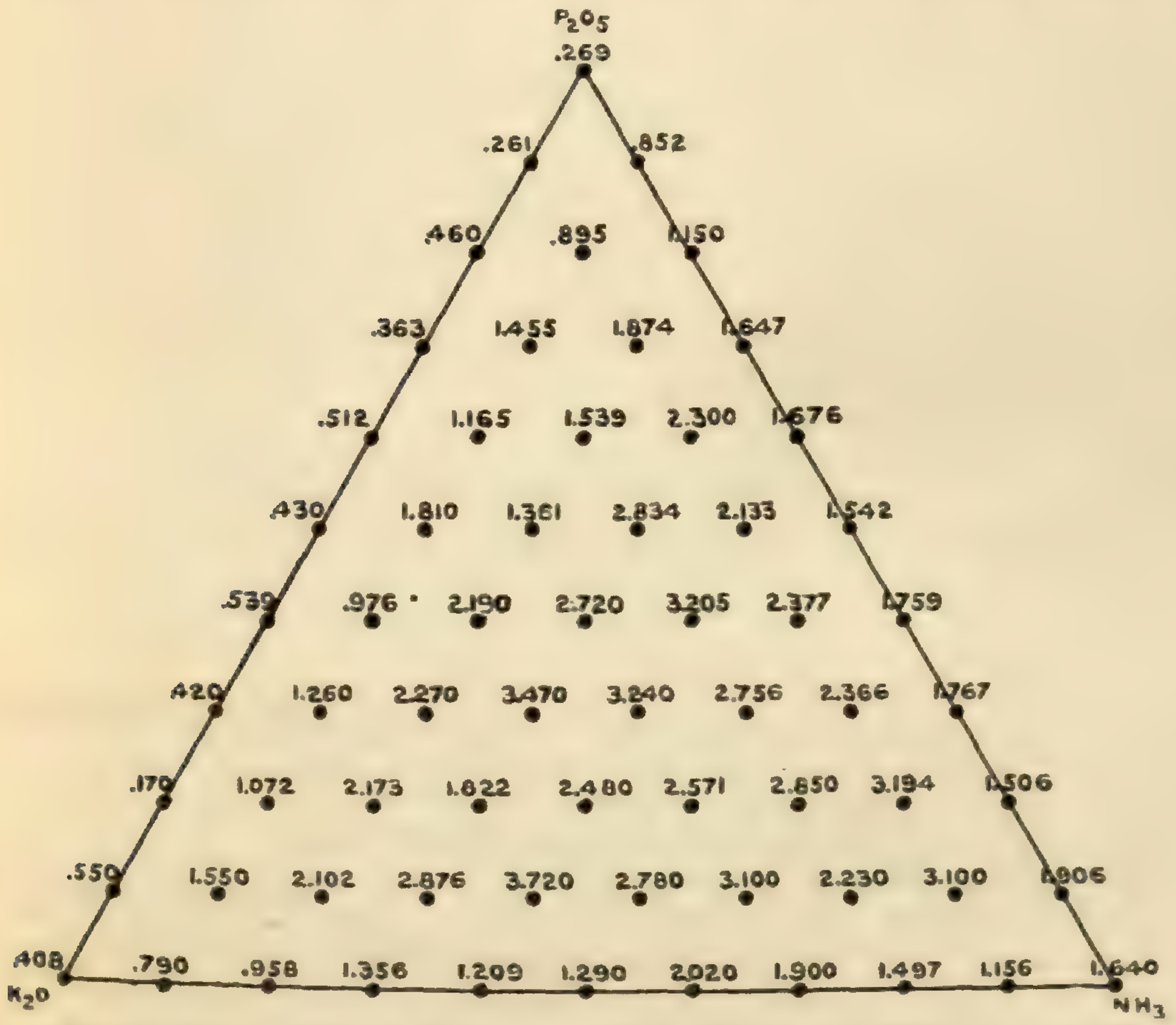

FIG. 6.—Green weight of wheat grown in 66 cultures with different proportions of P_2O_5, NH_3, and K_2O.

parts per million. After analysis the sum total of the three component parts was again calculated and the average concentration of these three elements was ascertained for the eight periods. These average concentrations will be found in the diagram in fig. 7. In practically all cases where dihydroxystearic acid was present, the concentration of the solution was not reduced as much as in the corresponding solution without dihydroxystearic acid, shown in fig. 4 of the former paper.

RATIOS OF P_2O_5, NH_3, AND K_2O FOUND IN THE VARIOUS CULTURES

In the diagram fig. 8 are given the original ratios of the fertilizer constituents, the ratios left in these solutions as shown by analysis, and the corresponding ratio of the removed constituents, as in the former paper. As before, the large dots in the diagram represent the original ratios according to the scheme previously

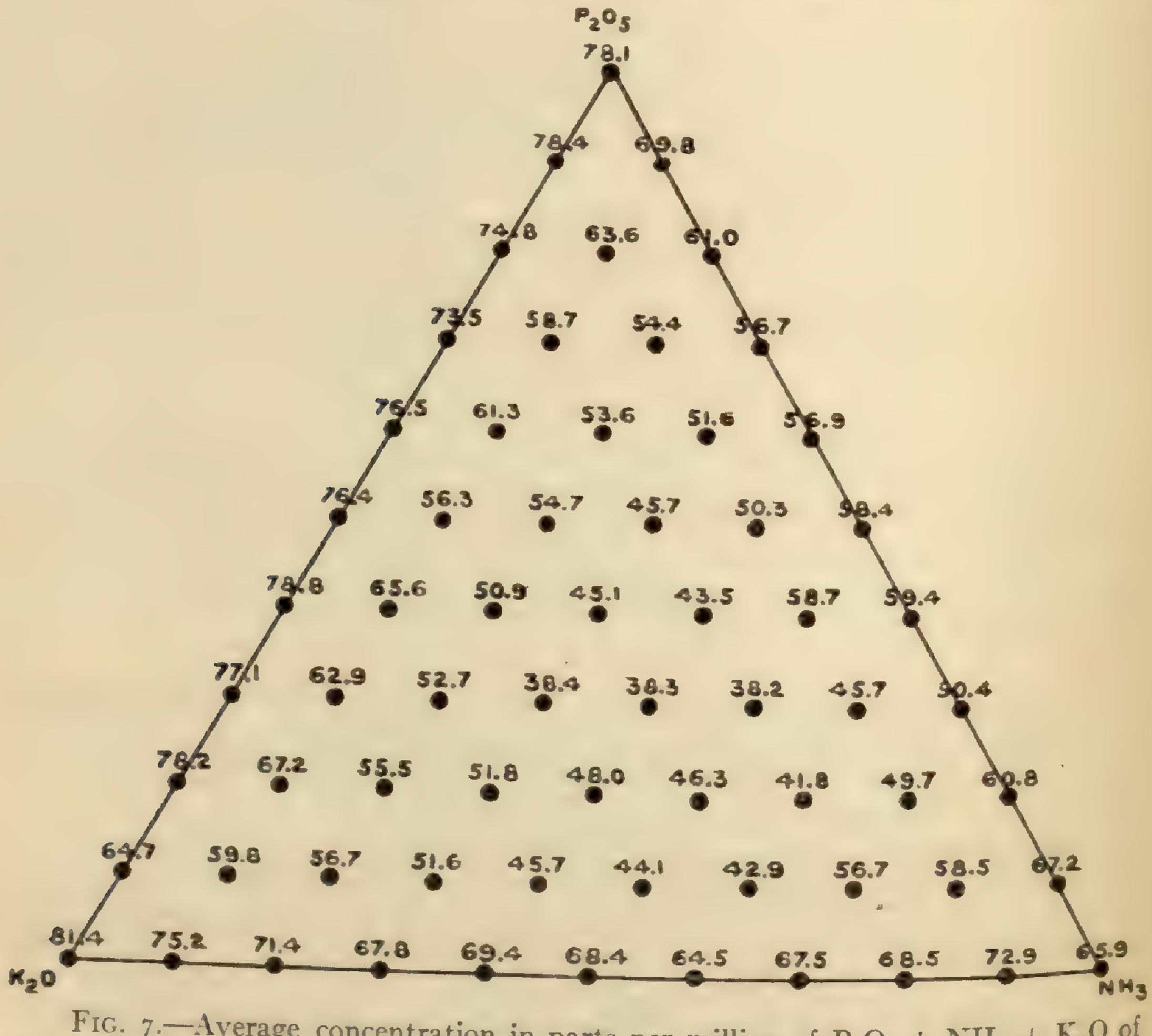

FIG. 7.—Average concentration in parts per million of $P_2O_5 + NH_3 + K_2O$ of the solution after the growth of 10 wheat plants; concentration of original solution was 80 p.p.m.

explained. The circles indicate the ratio left in the solution as shown by analysis, and the other end of the line indicated by an arrow shows the corresponding ratio of the removed materials.

In the former experiment without dihydroxystearic acid there was a decided tendency for these lines to converge toward a region somewhat below the center; that is, the solutions near this central area changed least in their ratio, and the farther the ratios were

removed from this central area originally, the more were they altered in the course of the experiment. This area was between the 10 and 20 per cent phosphate line, and the area of greatest growth occurred in this same region. It is in this region of greatest growth, therefore, that the greater absorption of nutrients took place with the least change in ratio; in other words, the solutions repre-

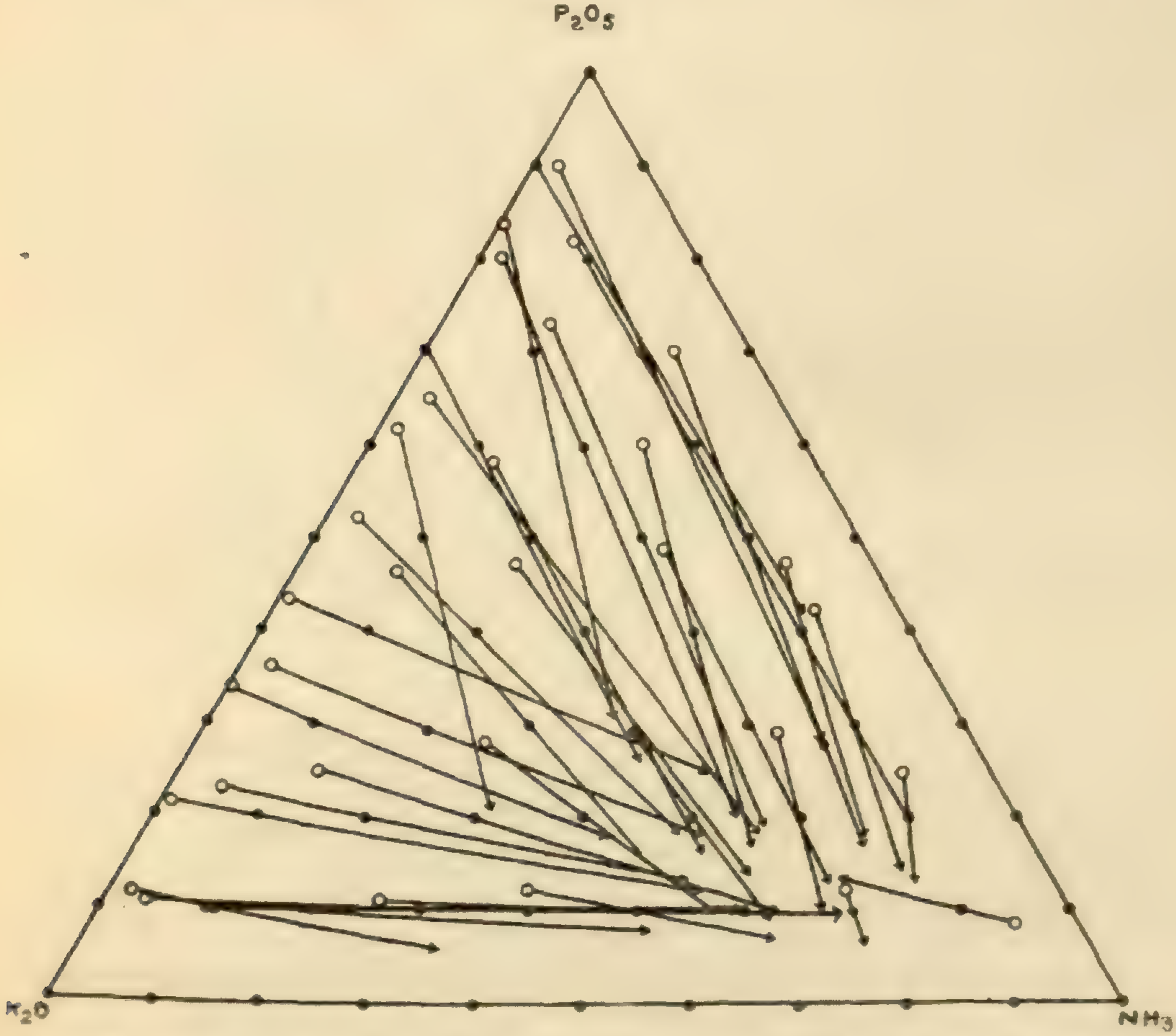

FIG. 8.—Showing the ratio of the original, the final, and the ratio of the loss of P_2O_5, NH_3, and K_2O from the culture solution; the dots indicate the ratio of the constituents in the original solution; the circles show the ratio of the constituents in the solution after growth; and the arrows show the ratio of the decrease.

sented by this region offered the best environment for plant development and the best ratios for the absorption of plant nutrients.

The diagram shown in fig. 8 for the experiment with dihydroxystearic acid shows on the whole a migration of the lines so that they point to an area somewhat nearer to the nitrate end of the triangle. It will be remembered from the data already discussed

that there is a tendency for the area of greatest growth under these conditions to be nearer this end.

In other words, when dihydroxystearic acid is present the results show a tendency for the ratios of the materials removed from the solution to fall nearer to the nitrogen end of the diagram than they do in the case of cultures where this substance is absent. This

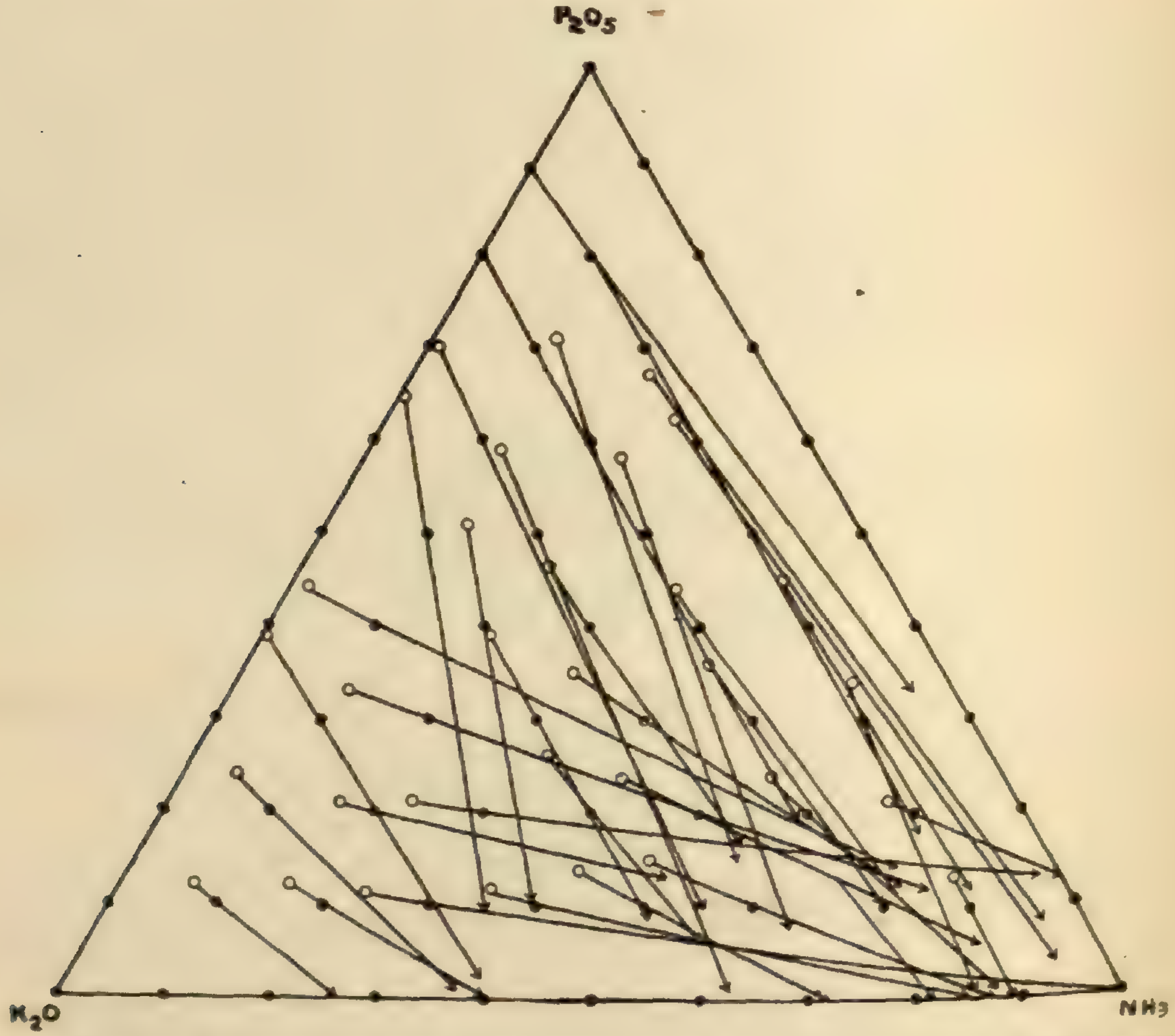

FIG. 9.—Showing the ratio of the original, the final, and the ratio of the loss of P_2O_5, NH_3, and K_2O from the culture solution, in the first period.

tendency is marked from the very first, as is shown by the diagram given in fig. 9 for the first period. Moreover, the points, for instance, of the 10 per cent mixture of P_2O_5 lie very low, and this tendency to lie lower than in the cultures which contained no dihydroxystearic acid is found throughout the experiment, though it is not equally marked in all periods. The average effect has already been given in the diagram fig. 8. The strong tendency

which is shown when this substance is present for a proportionately, and sometimes even absolutely, greater decrease in the nitrogen of the solutions, is strikingly shown in this first period (fig. 9). This varies somewhat from period to period; thus, for instance, in the fourth period, shown in fig. 10, the ratio change is fairly normal, though the usual tendency is seen again in the seventh period, a

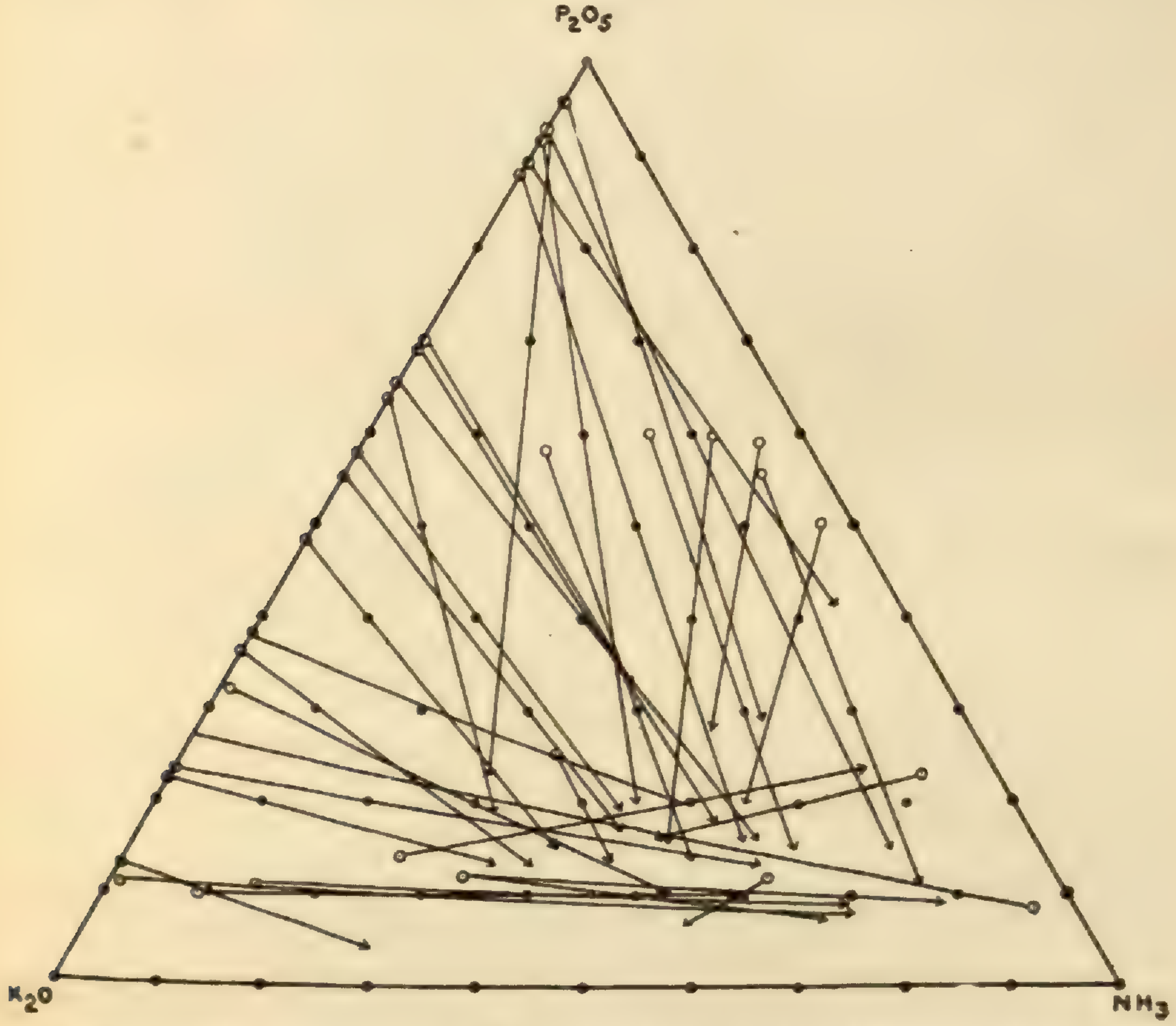

FIG. 10.—Showing the ratio of the original, the final, and the ratio of the loss of P_2O_5, NH_3, and K_2O from the solution, in the fourth period.

diagram of which is presented in fig. 11. These diagrams for the several periods illustrate rather well the general tendencies brought out by an examination of the analytical data. As a rule, beyond the second or perhaps the third period the diagrammatic representation of the result is on the whole uniform, but is influenced undoubtedly by the conditions of growth during any period; in other words, by weather and other conditions, which is shown perhaps quickest

in the nitrate removal from the cultures. The influence of light conditions on different days has already been discussed in the previous paper.

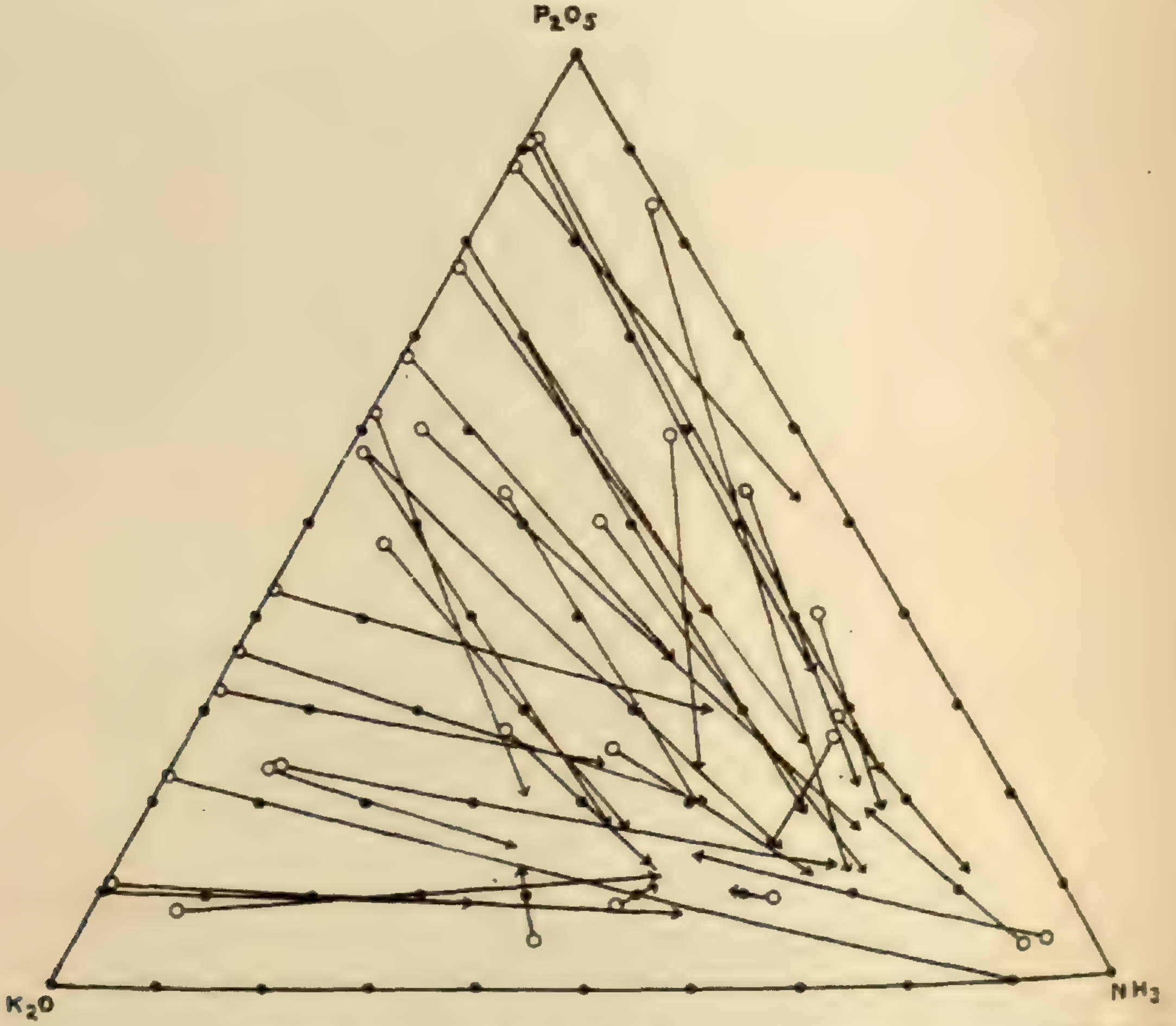

FIG. 11.—Showing the ratio of the original, the final, and the ratio of the loss of P_2O_5, NH_3, and K_2O from the solution, in the seventh period.

THE COMPARATIVE EFFECT PRODUCED ON THE DIHYDROXYSTEARIC ACID CULTURE SOLUTIONS BY THE FERTILIZER MIXTURES COMPOSED MAINLY OF P_2O_5, NH_3, AND K_2O RESPECTIVELY

In the experiment presented, as well as in two others in which both sets of cultures were grown simultaneously, there was noticed a more general tendency toward normal development of the plants in the presence of dihydroxystearic acid when the culture solutions contained all three of the fertilizer substances. It was further apparent that there seemed to be a tendency for more normal development in a region nearer to the nitrate end. In order to

trace out this matter, a comparison of the three experiments has been made and is hereby presented. In this way the solutions which contained in all cases 50 per cent or more P_2O_5 are considered in one group; all those which contained 50 per cent or more NH_3 in a second group; and those with 50 per cent or more K_2O in a third group. By grouping the cultures thus, an average result is obtained with the mainly phosphatic, mainly nitrogenous, and mainly potassic fertilizers.

A comparison of the average green weight in each of these groups of cultures was made with those in the corresponding groups in the cultures where dihydroxystearic acid was absent. The relative growths thus obtained, taking the growth without the dihydroxystearic acid as 100, are contained in table I.

TABLE I

SHOWING THE AVERAGE RELATIVE GROWTH MADE IN THE GROUP OF SOLUTIONS WITH DIHYDROXYSTEARIC ACID AND CONTAINING FERTILIZER SALTS HAVING THE COMPOSITION OF 50 TO 100 PER CENT OF ANY ONE OF THE COMPONENTS P_2O_5, NH_3, AND K_2O.

EXPERIMENT	RELATIVE GREEN WEIGHT (Green weight without dihydroxystearic acid = 100)		
	P_2O_5 50–100 per cent	NH_3 50–100 per cent	K_2O 50–100 per cent
1	49	67	43
2	60	62	62
3	71	68	61

In the first column is given the number of the experiment; in the second column the average relative green weight obtained in the solutions having mainly phosphatic fertilizers; in the third column the same result for the cultures of mainly nitrogenous fertilizers; and in the fourth column the results obtained when mainly potassic fertilizers were present. The results indicate, as was pointed out in discussing the experiment more fully described in this paper, that the mainly nitrogenous fertilizers enabled the plants to make a more normal growth than, on the whole, do the other fertilizers, although with the quantities of salts and harmful substance used in these experiments, the plants were by no means able to overcome the harmful effect entirely, if indeed this is possible.

This general relationship is even more strongly shown when the decreases in the concentrations of the solutions in these various groups are considered. The average decrease, in solutions with and without dihydroxystearic acid, for each group in each experiment, is shown in table II.

TABLE II

SHOWING THE AVERAGE DECREASES IN THE CONCENTRATION OF TOTAL CONSTITUENTS IN THE GROUP OF CULTURE SOLUTIONS CONTAINING FERTILIZER SALTS HAVING THE COMPOSITION OF 50 TO 100 PER CENT OF ANY ONE OF THE COMPONENTS P_2O_5, NH_3, AND K_2O, WITHOUT AND WITH DIHYDROXYSTEARIC ACID (ORIGINAL CONCENTRATION = 80 PARTS PER MILLION).

Experiment	50 100 per cent P_2O_5			50–100 per cent NH_3			50–100 per cent K_2O		
	Without	With	Decrease in dihydroxystearic acid solutions. Normal equals 100	Without	With	Decrease in dihydroxystearic acid solutions. Normal equals 100	Without	With	Decrease in dihydroxystearic acid solutions. Normal equals 100
1	27.8	17.6	63	35.4	24.0	68	34.0	13.9	41
2	28.9	24.6	55	30.3	34.6	114	38.5	30.8	80
3	27.8	23.8	85	35.9	32.0	89	45.0	31.0	69

The third column under each fertilizer group gives the relation between these decreases, the decrease in concentration when dihydroxystearic acid is absent being considered as the normal for comparison and equal to 100. A comparison of these relative effects shows that the mainly nitrogenous fertilizers give the highest results. In other words, the decrease with the nitrogenous fertilizers was more nearly like that observed under the normal conditions where dihydroxystearic acid was absent. This result may be interpreted to mean that the mainly nitrogenous fertilizers decreased the inhibitive effect of the dihydroxystearic acid, although it does not show whether this is a direct or an indirect effect; that is, whether there is an actual decrease of this inhibitive material or whether there is mainly the ability of the plant to withstand the attacks under these conditions. Attention has already been called to the fact that this substance when in soils is most easily destroyed by processes which promote oxidation, and it should be borne in mind that the mainly nitrogenous fertilizers are the ones which promote the most active root oxidation by the plants themselves. A study of the oxidation of roots in these

experiments showed that the dihydroxystearic acid interfered greatly with oxidation, and that this action was overcome to some slight extent in the center of the triangle but nearer to the nitrate end, thus showing perhaps that there is some correlation in these functions.

SUMMARY

The foregoing investigations have given the following results:

1. An organic soil constituent, dihydroxystearic acid, hinders the growth of wheat plants, when this is present in solution in pure distilled water.

2. The compound is also harmful in the presence of nutrient or fertilizer salts in all ratios of the fertilizer elements, P_2O_5, NH_3, and K_2O.

3. The compound is more harmful in those ratios of fertilizer elements not well suited for plant growth.

4. The harmful effect of the compound is the least in those ratios of fertilizer elements best suited for plant growth.

5. The compound appears to be relatively much less harmful in the presence of fertilizers mainly nitrogenous than in the presence of fertilizers mainly phosphatic or potassic.

6. The harmful compound modified greatly the removal of fertilizer elements from the solutions. The quantity of phosphate and potash removed was less in the presence of the compound, but the nitrate was not so influenced and on the whole the amount removed was even greater.

7. The compound modified both amount and ratio of the three fertilizer elements removed from solutions, the ratio being higher in nitrogen, which was also the most efficient fertilizer element in decreasing the harmful effect, as above mentioned.

8. The harmful compound has the additional effect of darkening the root tips, stunting root development, causing enlarged root ends, which are often turned upward like fish-hooks, and inhibiting strongly the oxidizing power of the roots.

9. Those fertilizer combinations which tend to increase root oxidation are also the combinations which overcome the harmful effects to the greatest extent.

BUREAU OF SOILS
U.S. DEPARTMENT OF AGRICULTURE
WASHINGTON, D.C.

SOME OBSERVATIONS ON CATALASE

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 139

CHAS. O. APPLEMAN

(WITH ONE FIGURE)

During the course of an investigation now in progress on the physiological behavior of enzymes in after-ripening of the potato tuber, it became necessary to investigate fully the best method for the quantitative determination of catalase in this organ. Some of the results thus obtained may be of general interest.

DISTRIBUTION AND FUNCTION OF CATALASE

SCHOENBEIN (1863) was the first to observe the power of various vegetable and animal extracts to decompose hydrogen peroxid with evolution of oxygen. He concluded that the enzymes occurring in the organisms were responsible for this phenomenon. This power of hydrogen peroxid decomposition was considered a more or less general property of enzymes until LOEW (1) showed that this property of tissues is due to a special enzyme to which he gave the name catalase. Its claim for a place in the category of enzymes at this time seems to be based wholly upon its sensitiveness toward heat, acids, and various poisons.

Catalase is probably the most widely distributed of any of the known enzymes. In fact, its occurrence is so general that LOEW concluded that there did not exist a group of organisms, or any organ, or even a single vegetable or animal cell, that did not contain some catalase. An enzyme of such general occurrence might naturally be supposed to possess an important function in the economy of nature. This may yet prove to be the case, but at present its position in this respect is uncertain. Little is even known regarding its mode of action on hydrogen peroxid. Definite knowledge on this point is limited to the fact that molecular instead of atomic oxygen results from the decomposition, and in this respect it differs from the other hydrogen peroxid catalysts.

Since the decomposition of hydrogen peroxid is the most important property of this powerful enzyme so widely distributed, it was suggested by LOEW that it may possess the function of preventing the accumulation of this toxic substance in the tissues. He conceived it possible and highly probable that hydrogen peroxid was produced in the living cells as the result of respiratory processes. USHER and PRIESTLY (9) were able to demonstrate the presence of hydrogen peroxid during photosynthesis if the catalase were previously destroyed. This fact would seem to support the above theory, but on the other hand, BACH and CHODAT (2) have shown that hydrogen peroxid is not a violent poison in tissues, since they have been able to cultivate certain plants in a medium containing 0.68 per cent of it. Catalase is found also in anaerobic organisms, a further fact which rendered the above conception untenable. Other authors have ascribed to catalase the function of protection against the peroxids of the organism, thus preventing injurious oxidations. It is unable, however, to decompose the substituted organic peroxids, such as ethyl hydroperoxid or the oxygenases (2).

Probably the most important question in connection with catalase at the present time is whether or not it may be considered as an oxidizing enzyme. It is true that it does not respond to the tests with the ordinary reagents for oxidizing enzymes, but this, according to LOEW, does not militate against its being an oxidizing enzyme, since the action of oxidizing enzymes is sometimes quite specific. He claims that a characteristic oxidation by catalase is produced with hydroquinone and also some with glucose and citric acid. SHAFFER (3) thinks that this quinone-formation was undoubtedly due to the presence of some enzyme other than catalase, since he found that animal tissues always contain catalase, but frequently possess no power to oxidize hydroquinone.

According to the BUCHNER and MEISENHEIMER (4) conception of alcoholic fermentation, the sugar is converted into lactic acid by the zymase, and the lactic acid in turn is split up into alcohol and carbon dioxid by a lactacidase enzyme. In a recent work KOHL (5) claims to have proved, for yeast fermentation at least, that catalase performs the function of the zymase in the above

conception, and if no zymase is present the lactic acid is oxidized to oxalic acid by oxidizing enzymes. If zymase is present, it splits the salts of lactic acid up into alcohol and carbon dioxid, the work of the lactacidase according to BUCHNER and MEISENHEIMER. This work of KOHL'S, if confirmed, brings to catalase a very important rôle in physiological processes as an oxidizing enzyme.

METHODS

The following method was employed in all the catalase determinations except where otherwise stated. The apparatus used is shown in fig. 1. The potato was grated rapidly on a nutmeg grater with frequent dipping of the grated surface into calcium carbonate. After grating, the pulp was ground for two minutes in a mortar with quartz sand. The extract was then pressed lightly through two layers of absorbent cotton and one of cheese cloth. After mixing, 1 cc. was withdrawn immediately and placed into the bottle used for the determination, and 1 cc. of *cold* water added. The apparatus was then placed into a water bath at 20° C. After the apparatus had attained the temperature of the bath, 5 cc. of Oakland 3 per cent hydrogen peroxid (dioxygen) were run into the bottle from the separating funnel *2*. The stopcock *a* was opened 15 seconds before the minute. On the minute, shaking was begun and continued with as much regularity as possible to the end of the experiment. On the quarter-minute the stopcock *b* was opened and the oxygen allowed to run into the gas burette. On the half-minute the stopcock *b* was closed and a reading made at the burette. Stopcock *c* was now opened until the menisci in the burettes were again level. At the three-quarter mark the stopcock *b* was opened again and closed on the minute for a reading. This procedure was continued with readings every 30 seconds for three minutes. With longer periods the experimental error becomes greater on account of lack of uniform shaking.

EFFECT OF GRINDING WITH CALCIUM CARBONATE

GRÜSS (10) reports that it is impossible to make quantitative determinations of catalase in the fresh potato extract on account of the rapid degeneration during the grinding and subsequently.

If the potato is ground with calcium carbonate to neutralize the acids freed by the grinding, and 5 cc. of the extract is at once diluted with 50 cc. and kept at a temperature of 20° C. or below, this rapid degeneration may be overcome and comparable results obtained

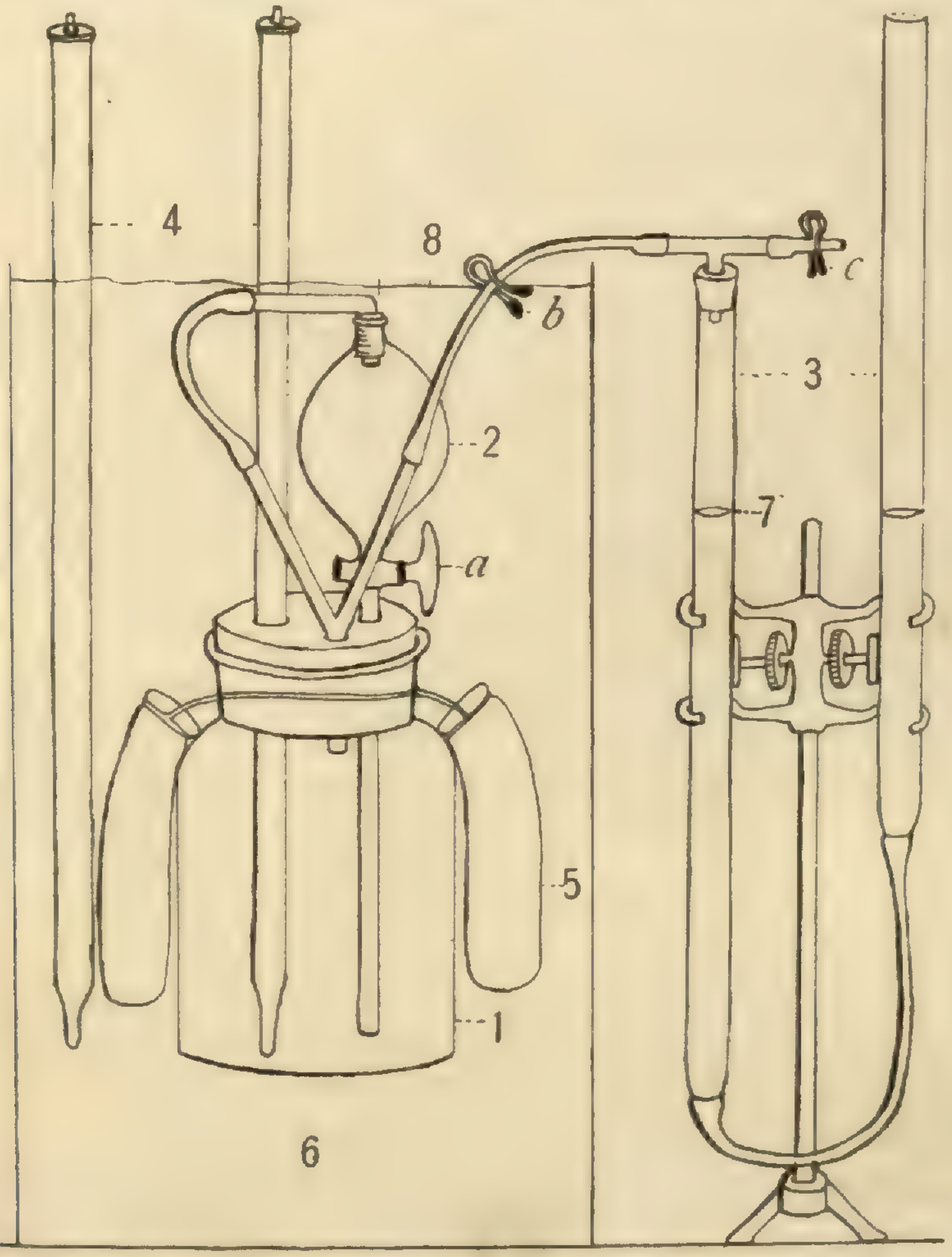

FIG. 1.—Apparatus used for catalase determinations: *1*, thin-walled bottle; *2*, separatory funnel; *3*, gas burettes; *4*, thermometers; *5*, weights; *6*, water bath; *7*, water meniscus; *8*, water level in bath; *a*, stopcock for running the hydrogen peroxid into bottle; *b*, stopcock for controlling the flow of oxygen into the burette; *c*, stopcock for equalizing the air pressure in burettes.

without any difficulty. It is necessary, however, to maintain the same period of time for grinding, as there is a slight degeneration even under the above conditions, due to another cause, as we shall see later. The shaking must also be constant and uniform during the determination.

Table II shows the effect of grinding and storage with calcium carbonate. After grinding two potatoes of equal weight, one with

and the other without calcium carbonate, they were stored at 0° C. for 34 days. At the end of this time, 200 cc. of water were

TABLE I

LOSS OF CATALASE DUE TO ACIDS IN THE EXTRACT

POTATO	CC. O_2 EVOLVED IN 1-MIN. PERIODS					TOTAL CC. O_2 IN 5 MIN.
	1st	2d	3d	4th	5th	
Ground without $CaCO_3$.....	3.2	3.0	2.3	1.7	1.3	11.5
Same extract after standing 15 min.....	1.7	1.8	1.6	1.3	1.0	7.4
Ground with $CaCO_3$.....	6.4	5.9	4.6	3.6	2.8	23.3
Same extract after standing 90 min.....	6.5	5.8	4.3	3.3	2.6	22.5

added to each flask containing the pulp, and 5 cc. of this dilution and 5 cc. of hydrogen peroxid were used for the determination in each case.

TABLE II

EFFECT OF STORAGE FOR 34 DAYS AT 0° C. WITH AND WITHOUT CALCIUM CARBONATE

POTATO	CC. O_2 EVOLVED IN 30-SEC. PERIODS						TOTAL CC. O_2 IN 3 MIN.
	1st	2d	3d	4th	5th	6th	
Ground without $CaCO_3$.....	0.3	0.4	0.4	0.4	0.4	0.4	2.3
Ground with $CaCO_3$	12.4	10.9	8.9	6.9	5.4	4.0	48.4

FILTERING

Approximately 50 per cent of the total catalase will pass through an ordinary filter paper, but none through a Chamberland-Pasteur filter. The first fact seems to indicate the existence of an insol-

TABLE III

EFFECT OF FILTERING THROUGH ORDINARY FILTER PAPER

EXTRACT OF POTATO TUBER	CC. O_2 EVOLVED IN 30-SEC. PERIODS						TOTAL CC. O_2 IN 3 MIN.
	1st	2d	3d	4th	5th	6th	
Filtered through filter paper	2.8	2.4	1.8	1.5	1.3	1.1	10.9
Portion of same extract unfiltered.....	4.0	4.5	3.8	3.2	3.1	3.4	22.6

uble (α-catalase) and a soluble (β-catalase) form. KOHL finds the same true of yeast catalase, and LOEW believes it a general char-

acter of vegetable catalase. The size of the molecule of the latter prevents its passage through a Chamberland-Pasteur filter.

Table IV also shows the effect of filtering and the necessity of thorough mixing of the extract before taking the sample for a total catalase determination.

TABLE IV

EFFECT OF FILTERING AND SETTLING

EXTRACT OF POTATO TUBER	CC. O_2 EVOLVED IN 30-SEC. PERIODS						TOTAL CC. O_2 IN 3 MIN.
	1st	2d	3d	4th	5th	6th	
Unfiltered	12.2	9.5	7.0	5.0	4.0	3.2	40.9
Supernatant liquid after settling	5.4	4.5	3.5	3.0	...	...	....
After mixing, 20 min. later	11.9	9.5	6.9	5.3	3.8	3.2	40.6
Filtered, 40 min. later	5.5	4.8	3.5	2.7	2.1	1.7	10.3

TABLE V

EFFECT OF FILTERING THROUGH A CHAMBERLAND-PASTEUR FILTER

EXTRACT OF POTATO TUBER	CC. O_2 EVOLVED IN 30-SEC. PERIODS						TOTAL CC. O_2 IN 3 MIN.
	1st	2d	3d	4th	5th	6th	
a) Unfiltered	24.8	22.8	19.3	16.8	14.8	13.5	52.
b) Filtered through Chamberland filter	0.	0.	0.	0.	....	....	....
c) Residue of (*b*) made up to same volume as (*a*)	25.	22.3	19.3	16.7	14.8	13.5	51.6

TEMPERATURE RELATIONS

Catalases from different sources show considerable variation in temperature relations, the point of total destruction in the cases reported ranging from 65° C. to 80° C. In potato catalase, however, destruction is complete when the temperature reaches 50° C.

The VAN'T HOFF velocity coefficient for hemase has been found to be 1.5. The same figure applies to potato catalase, but is evident only from 0 to 10°. At 20° a destruction of the catalase begins, which renders the accelerating effect of higher temperatures upon the peroxid decomposition impossible of manifestation.

The diminishing coefficient indicated in table VI is due to actual destruction of the catalase, as will be seen by table VII, which also shows that the destruction at moderate temperatures is not due

to impurities in the hydrogen peroxid. Some substance in the potato may be freed by the grinding and brought into contact

TABLE VI

JOINT EFFECT OF ACCELERATION AND DESTRUCTION BY RISING TEMPERATURE

Range of temperature	0–10°	10–20°	20–30°	30–40°
Velocity coefficients .	1.5	1.1	0.85	0.18

with the catalase, which effects its slow destruction. It is interesting to note in this connection, however, that SENTER (**6**) found hemase to be oxidized at all temperatures above 0° C.

TABLE VII

AMOUNT OF CATALASE DESTRUCTION AT 30° C. FOR 15 MIN. OVER THAT AT 20° C. FOR THE SAME PERIOD

POTATO TUBER EXTRACT	DETERMINATION TEMP.	CC. O_2 EVOLVED IN 30-SEC. PERIODS						TOTAL CC. O_2 IN 3 MIN.
		1st	2d	3d	4th	5th	6th	
a) Exposed to 30° C. only during determination of catalase	30° C.	14.8	14.7	14.1	13.2	12.5	11.9	21.2
b) Exposed to 30° C. during exp. (*a*), then cooled to 20° C. for determination	20° C.	15.0	14.5	13.7	13.3	12.7	12.4	21.6
c) Not exposed above 20° C.	20° C.	15.9	15.1	14.7	13.9	13.3	12.8	25.7

DESTRUCTION OF THE CATALASE DURING THE REACTION WITH HYDROGEN PEROXID

Potato catalase is not unlimited in its power to effect the decomposition of hydrogen peroxid. Table VIII shows not only the above fact, but also would seem to indicate that it is consumed in the reaction and that a given amount is capable of decomposing a definite amount of hydrogen peroxid.

The total extract of a potato weighing 50 grams was diluted to 500 cc. with water, and 5 cc. of this extract were allowed to act upon 1 cc. of 1.5 per cent hydrogen peroxid until less than 0.1 cc. of oxygen was evolved in 5 min. Another cubic centimeter of hydrogen peroxid was then added and the reaction allowed to run to the same point. This procedure was continued until the addition of a cubic centimeter of hydrogen peroxid produced only 1.1 cc. of oxygen in 25 min.; 6 cc. were required to bring the reaction to

this point. A fresh portion of 5 cc. of the extract, which had stood at the same temperature, was now allowed to act upon 6 cc. of hydrogen peroxid at the same time, with the result that approximately the same amount of oxygen was evolved as the total produced when 6 cc. were added in successive lots of 1 cc. each. The experiment was repeated several times with different extracts and dilutions, with practically the same result in every case.

TABLE VIII

CONSUMPTION OF THE CATALASE DURING THE REACTION WITH HYDROGEN PEROXID

POTATO TUBER EXTRACT	CC. O_2 EVOLVED WHEN H_2O_2 WAS ADDED IN SUCCESSIVE LOTS OF 1 CC. EACH						TOTAL CC. O_2 EVOLVED	TOTAL CC. O_2 EVOLVED WHEN 6 CC. WERE ADDED IN BULK
	1st	2d	3d	4th	5th	6th		
5 cc. extract	8.2	6.5	6.3	5.4	4.0	1.1	31.6	
5 cc. same extract	...	...	...	...	...	...	....	31.8

The destruction or degeneration of the catalase would be slight during the time of the experiment in the above dilute neutral solution at 20°. Admitting a slight destruction, it would be the same in both cases, and would therefore not affect the general result. KASTLE (7) suggests that catalases, like peroxidases, may combine with the hydrogen peroxid to form an unstable holoxid derivative, as $K+H_2O_2=H_2KO_2$. This might in turn oxidize the catalase itself (K) which may be more readily oxidizable than any of the peroxidase reagents, in which event we would have $H_2KO_2=H_2O+KO$. This conception is in striking harmony with the facts indicated in the above table, and with the fact that the reaction is decidedly an exothermal one.

RELATION TO FUNCTIONAL ACTIVITY

There is considerable evidence from animal tissues that catalase activity bears a relation to functional activity of the structure. Such a relation seems to exist in the potato, at least in respect to respiratory activity. Extracts from potatoes which have been kept for several days at 0° C. show a decided decrease in catalase activity. MÜLLER-THURGAU (8) has also shown that respiration is greatly reduced in such potatoes.

Catalase activity is greater at the end than at the beginning of the rest period. It is also greater in the large mature potatoes

TABLE IX

DECREASE IN CATALASE ACTIVITY AFTER STORAGE AT 0° C.

WEIGHT OF WHOLE POTATO	TIME OF STORAGE	TEMP. OF STORAGE	CC. O_2 EVOLVED IN 30-SEC. PERIODS						TOTAL CC. O_2 IN 3 MIN.
			1st	2d	3d	4th	5th	6th	
219 gm.....	28 days	20° C.	12.8	10.5	7.5	5.5	4.3	3.8	44.4
214 gm.....	28 days	0° C.	7.5	6.9	5.2	4.0	3.1	2.6	29.3

than in the small immature ones. This is true to a much greater extent in new potatoes than old ones. MÜLLER-THURGAU (8) found that these same relations exist in regard to respiration.

TABLE X

RELATION OF CATALASE ACTIVITY TO AGE AND SIZE OF THE POTATOES

POTATO AT	WT. OF POTATO	CC. O_2 EVOLVED IN 30-SEC. PERIODS				TOTAL CC. O_2 IN 2 MIN.
		1st	2d	3d	4th	
Beginning of rest period ..	100 gm.	17.5	16.3	14.5	13.6	21.9
Beginning of rest period ..	400 gm.	27.3	23.8	19.9	16.9	47.9
End of rest period.....	147 gm.	35.5	26.0	19.1	15.0	55.6
End of rest period.....	540 gm.	39.0	27.5	19.1	14.5	60.1

In table XI equal weights of morphologically similar pieces of new and old potatoes of about the same weight were ground, washed into a volumetric flask, and made up to 250 cc. with water. After thorough shaking, 5 cc. were withdrawn for the test, using 5 cc. of hydrogen peroxid as before.

TABLE XI

CATALASE ACTIVITY AT BEGINNING AND END OF REST PERIOD

POTATO AT	CC. O_2 EVOLVED IN 30 SEC. PERIODS						TOTAL CC. O_2 IN 3 MIN.
	1st	2d	3d	4th	5th	6th	
Beginning of rest period	16.5	16.0	14.8	14.0	13.5	12.9	27.7
End of rest period.....	21.2	20.2	18.0	16.1	14.7	13.8	44

The above facts do not prove a causal relation between catalase and respiration, but they are highly suggestive, especially in the

light of KOHL'S recent claims for catalase as an important enzyme in alcoholic fermentation, and therefore most likely in respiratory processes.

SUMMARY

1. Comparable quantitative determinations of potato catalase can be made in the fresh extracts, if the material is ground with calcium carbonate, the extract diluted immediately with ten parts of water to one of extract, kept at 20° C. or below, and the same time maintained for the grinding of the potato and the catalase determination.

2. An insoluble (α-catalase) and a soluble (β-catalase) form may be separated by ordinary filter paper. Approximately 50 per cent of the total passes through. None will pass through a Chamberland-Pasteur filter.

3. The VAN'T HOFF velocity coefficient for potato catalase is 1.5 from 0° C. to 10° C. At higher ranges of temperature there is an apparent progressive decrease in the velocity coefficient. This is due to actual destruction of the catalase, which is not due in the main to impurities in the hydrogen peroxid or to oxidation by the hydrogen peroxid.

4. Potato catalase is not unlimited in its power to effect the decomposition of hydrogen peroxid. It seems to be consumed in the reaction and a given amount is capable of decomposing a definite amount of hydrogen peroxid.

5. The catalase activity bears a relation to the respiratory activities in the potato, decreasing under the same conditions as respiration.

I wish to acknowledge my indebtedness to Dr. WILLIAM CROCKER, under whose supervision this work was pursued.

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TWIN HYBRIDS (*LAETA* AND *VELUTINA*) AND THEIR ANATOMICAL DISTINCTIONS

FRANK M. ANDREWS

Twin hybrids are produced according to DEVRIES "by the combinations *Oenothera biennis*×*O. Lamarckiana*, and *O. muricata*×*O. Lamarckiana*, and by those of some of their derivatives."[1] Besides *laeta* and *velutina* I shall describe here *O. Lamarckiana* and *O. biennis*. *O. biennis*, along with some other species, was introduced into Europe a long time ago. The origin of *O. Lamarckiana*, or large-flowered evening primrose, is involved in obscurity. In an old potato field near Hilversum, in the year 1886, DEVRIES[2] found a great many specimens of *O. Lamarckiana* which were observed to be in a state of mutability. I have visited this primrose field to observe and collect specimens. There are comparatively few of them left, due to the fact that they are rapidly being crowded out by pine trees that have been planted there. It is apparently only a question of a little time, unless something intervenes, until they will have disappeared entirely from that locality. *O. Lamarckiana* produced new forms by mutation, not only in the wild state in the field near Hilversum, but also in cultivation. This latter fact was proved by transferring rosettes from the field to the garden, where the plants could be protected and watched throughout their entire existence. This method, together with that of sowing the seeds[3] of these plants under controlled conditions, has allowed quite a number of mutants to assert themselves and to be recognized. Unless such methods as were introduced by DEVRIES in his garden at Amsterdam are followed, the detection of a mutation is much more apt to be only accidental. Furthermore, these methods when used for rapid multiplication in the garden under controlled and protected conditions may also be conducive to an increase of mutants, and hence their more certain and frequent recognition. For "such a rapid multiplication in the course of a comparatively few years" (as

[1] DEVRIES, HUGO, On twin hybrids. BOT. GAZETTE **44**:401–407. 1907.

[2] DEVRIES, HUGO, **Mutationstheorie 1:152, 401–407.**

[3] DEVRIES, HUGO, Species and varieties, p. 525. 1905.

was noticed with *O. Lamarckiana* near Hilversum) "may perhaps be," says DEVRIES, "one of the conditions for the appearance of a mutable period."[4] The number of new forms that have arisen and been detected by DEVRIES in the genus *Oenothera* since his discovery of the mutating *O. Lamarckiana* at Hilversum in 1886 is already considerable.

The following description of the forms *O. Lamarckiana*, *O. biennis*, *laeta*, and *velutina* represents in each case the average state of affairs as shown by a great number of examined specimens.

O. Lamarckiana is an erect, strong plant. Its stem is cylindrical, 1–1.5 cm. in diameter, 1.5 or more meters in height, and sparsely covered with coarse hairs. Some of the hairs on the stems are glandular. The main stem is more or less branched at the top, and also has a tendency to produce smaller branches at the bottom when it grows in an open situation. All of the secondary branches may produce flowers.

The leaves are somewhat broadly lanceolate, dark green, their margins distinctly dentate, and the lower ones strongly petioled. Both the upper and the lower surfaces, especially in the adult forms, are conspicuously undulated or wrinkled, and only slightly pubescent.

In order to get buds showing as great uniformity as possible, they were chosen just before they were ready to open. The buds of *O. Lamarckiana* are the largest of any of the three forms mentioned, being about 5.5 cm. in length, about 1 cm. broad near the base, and tapering slowly upward to a width of about 2 mm. at the top. They are slightly pubescent. This pubescence of the buds of all the three forms studied consists of two kinds of hairs, a small, thin-walled, cylindrical hair, and a larger, thick-walled, pointed one. In *O. Lamarckiana* both of these hairs are much larger than in any of the other forms of *Oenothera* to be described, and especially is this true of the pointed hairs. The buds are almost circular in cross-section.

The flowers are large and bright yellow, and arranged rather closely together in a broad spike. Each flower is subtended by a sessile bract and stands singly. The ovary is partly glandular-pubescent, and the four lanceolate sepals are strongly reflexed, gen-

[4] DEVRIES, HUGO, Mutationstheorie 1:152.

erally more or less united at the top, and somewhat pubescent. The calyx tube is a little longer than the sepals. The cell walls of the epidermis of the sepals of *O. Lamarckiana*, especially the inner epidermis, are very irregular and zigzag in form. At the angles of these zigzag places the walls of the inner epidermis are marked by conspicuous thickenings. In the case of the outer epidermis the thickenings at these places extend away from the main wall as T-shaped processes. The same is true, but to a slightly less degree, for the inner and outer epidermis of the petals. The four very large, broadly obovate, entire petals are very conspicuous, and almost or quite equal the length of the calyx tube. One of the distinguishing features of *O. Lamarckiana* is the tall stigma, which far exceeds in height the stamens, and on this account self-pollination cannot occur. The anthers of *O. Lamarckiana* open in damp or rainy weather as well as on clear days, but this, as we shall see later, is not true of some forms, as for example the twin hybrids. This can be accomplished in the parent species, *O. Lamarckiana*, because at maturity the tissues of the cell walls of the anther are completely differentiated and become free, so that the outer wall may open out in the usual way.

The capsules are four-celled and open by as many valves at maturity. The pubescence on the capsules is not so dense as on the ovary. As the old flowers disappear and new ones appear, long rows of capsules are left on the older parts of the spike.

Oenothera biennis is not as stout as *O. Lamarckiana*. Its stem is erect, cylindrical, branching, and sparsely covered with coarse but non-glandular hairs. It is branched, is about 1 cm. in diameter, and 1–1.5 meters in height.

The leaves are dark green, broad (somewhat more so than in *O. Lamarckiana*), about three times as long as wide, with margins slightly wavy, and all of the stem leaves are petioled. In the last two respects the Holland species is somewhat different from the more narrow-leaved American species of *O. biennis*, which has only the "lowest petioled"[5] and the margins "repand-denticulate."[5] These are among the differences that show that the form *O. biennis*, which is very common in the United States, is not the same as the *O. biennis*

[5] BRITTON AND BROWN, Flora of the northern U.S. and Canada **2**:486.

of Europe. The upper and lower surfaces of the lower leaves are not wrinkled as we have seen in *O. Lamarckiana*, and are less hairy.

The buds are much smaller than those of *O. Lamarckiana*, averaging 1.5 cm. long, 6 mm. wide at the base, and 1.5–2 mm. wide at the top. Besides being smaller, they are different in form from those of *O. Lamarckiana*. One side of the bud is rather straight, and the other more or less gibbous. Comparing this with the American species, as shown by BRITTON and BROWN'S figure,[6] there is another difference, for in the American forms the buds are larger and more pointed, especially at the apex, than in the Holland type. The hairs on the buds are only about half the size of those of *O. Lamarckiana*.

The flowers are much smaller than those of *O. Lamarckiana* and are bright yellow. Each flower stands in the angle of a nearly sessile bract on the rather narrow spike. The calyx tube in this form is 1.5–2 times the length of the reflexed sepals. The density of the pubescence on the sepals is about the same as for *O. Lamarckiana*. The irregularity shown in the epidermal cell walls of the sepals is much less in *O. biennis* than in *O. Lamarckiana*, and especially is this true of the inner epidermal cell walls, which are only wavy, and in which the thickenings are almost completely absent. The cells of the outer epidermis are also decidedly smaller and have but few thickened places.

The four petals are broad, slightly unequally lobed, somewhat indented at the apex, and larger than the sepals. The cells both of the inner and outer epidermis are smaller, more regular in form, and are, especially those of the inner epidermis, almost devoid of the angular thickenings shown by *O. Lamarckiana*.

One of the chief differences in the flowers of *O. Lamarckiana* and *O. biennis* is that in the latter the stamens are of the same height as the stigma, and the anthers are in contact with the stigma in the bud. Therefore self-pollination nearly always results, whereas in *O. Lamarckiana* it was generally brought about by insects. The four anther cells do not always open simultaneously, but some may have partly opened and shed their pollen before the opening process in the other cells has begun. The ovary is four-celled and pubescent.

[6] BRITTON AND BROWN, *op. cit.* 2:486. *fig.* 2579.

The capsules are almost pressed against the stem. They are about 24 mm. long, somewhat pubescent, and remain as the flowers disappear in long rows on the spike, as in *O. Lamarckiana.* These capsules of *O. biennis*, according to BRITTON and BROWN'S figure,[7] seem to be differently curved and more pointed toward the top. Instead of the usual number of parts of the flower of *O. biennis*, I have observed some where there were three sepals, three petals, six stamens, and three stigmas. Deviations of a similar kind I have noticed in other plants.[8]

The stem of *laeta* is branched, about the same height as that of *O. biennis*, and almost intermediate between the two parents as to stoutness and pubescence.

The leaves are broad, bright green, and while wrinkled they are hardly as much so as in *O. Lamarckiana.* They are considerably more pubescent than those of *O. biennis* and slightly more so than those of *O. Lamarckiana.*

The buds differ in size and form from those of the other forms. They are more pubescent than in *O. Lamarckiana* or *O. biennis*, smaller than in *O. Lamarckiana*, and larger than in *O. biennis.* In cross-section they are almost round.

The hairs of the buds and other parts of the plant are distinctive as to size, for they are considerably longer than those of either *O. biennis* or *velutina*, but smaller than those of *O. Lamarckiana.*

The lanceolate and strongly reflexed sepals are about three-fourths of the length of the calyx tube, and are somewhat more pubescent than in any of the preceding forms.

Both the form and the size of the cells of the outer and inner epidermis of the sepals, as well as of the petals, of *laeta* are different from those of either of the three other forms mentioned here.

The relative size of the stamens and style is another distinctive feature, for the style is somewhat higher than the stamens, being less pronounced than in *O. Lamarckiana.* Both the stamens and the style are much smaller than in *O. Lamarckiana.* The stamens about equal in size those of *O. biennis* and *velutina.* The anther cells behave differently from any of the previously described forms, in

[7] BRITTON AND BROWN, *op. cit.* 2:486. *fig. 2579.*

[8] See my paper in Proc. Indiana Acad. Sci. for 1905 and 1906.

that in damp or rainy weather they do not open at all, and sometimes very imperfectly even on sunny days. I have observed anthers, one or two of whose cells never open, and the remaining cells do so only partly. The anthers seem to develop normally in every respect except that the tissues do not become differentiated completely at the usual point of opening, so as to allow the escape of the abundantly formed pollen grains in the ordinary way. It was often necessary to exert strong pressure on the cover glass before the anther wall would separate at the usual place, and this was true even in thin cross-sections.

The ovary of *laeta* is more pubescent than that of *O. Lamarckiana* or *O. biennis*.

The capsule is about the size of that of *O. Lamarckiana*, but different in form from either parent. They form very long spikes of fruit before the close of the flowering period.

Velutina, the other twin hybrid form, is also distinctly different from *laeta* and all other forms.

Its stem is about the same height as that of *laeta*, somewhat more branched, and light grayish, due to the dense pubescence. The hairiness of the whole plant is much more pronounced than in any of the other forms described, and this fact alone would serve to distinguish it from any of them. The stem is not quite so stout as that of *laeta*, and the aspect of the whole plant is somewhat less vigorous.

The leaves are grayish green, narrow (more so than in *laeta*), trough-shaped, tapering toward each end, and much more pubescent than the leaves of any of the other forms.

The buds are shorter than those of *laeta*, but have a greater diameter and are much more hairy. The hairs from the buds, as in the other types, are of two forms, cylindrical and pointed. The cylindrical hairs are only a little larger than those of *O. biennis*, but smaller than in the other types. The pointed hairs are exceeded in size by those of *O. Lamarckiana*, but are larger than those of *O. biennis* and *laeta*. These pointed hairs of *velutina* differ from those of *laeta* and all the other forms in another respect. In all the other forms the pointed hairs are smooth, but in *velutina* they are densely covered by numerous and conspicuous elevations.

The flowers are somewhat smaller than those of *laeta*.

The sepals are only about one-half the length of the calyx tube, whereas in *laeta* they are about three-fourths of its length. This difference is very evident on comparison. The sepals of *velutina* are also much more hairy than any of the other forms.

The cells of the outside epidermis of the sepals of *velutina* are about uniform in size with those of *laeta*, but the walls are much stronger. The cells of the inner epidermis are more uniform in size than in *laeta*.

The petals are more deeply indented at the top than in *laeta*, are somewhat smaller, and light yellow. The cells of the inner and outer epidermis are more nearly isodiametric than in *laeta*, and their cell walls are much more zigzag, and thickened at the angles.

The stamens are the same length as the stigmas. In this respect they differ strikingly from *laeta* and *O. Lamarckiana*, but resemble *O. biennis*. As in *laeta*, they open some of their anther cells at least, on sunny days, but on damp and rainy days they remain closed. I have noticed instances, as in *laeta*, where some of the anther cells never open, no matter how ideal the conditions. I have found it necessary to use considerable force in order to cause even thin cross-sections of the anthers to open their cells. This, as in *laeta*, is due to the fact that the tissues at the point of opening never separate, but remain more or less completely grown together. This non-opening of the anthers of *Oenothera* forms, however, is not confined to those mentioned above. I have visited another primrose garden at Haarlem which is conducted by Mr. A. R. SCHOUTEN and Mr. J. JESWIET. In this garden are grown, among other forms, *O. scintillans* and *O. gigas*, and Mr. JESWIET kindly informed me that they often find it necessary to open the anthers with a needle in order to free the pollen. Much of this pollen, as in our twin hybrids, is not sterile, but in some cases would never escape naturally from the anthers. Mr. JESWIET tells me that of the types they have at Haarlem all of the anthers of *O. scintillans* must be opened with a needle to obtain the pollen, and also many of the anthers of the form *O. gigas*.

The ovary of *velutina* exceeds all the other forms as to density of pubescence.

The capsule resembles that of *laeta*, but is curved near the top. It is strikingly different from *laeta* in regard to its denser pubescence.

One further difference remains to be recorded in reference to the petals of the flowers of *O. Lamarckiana*, *O. biennis*, *laeta*, and *velutina*. As we look at these flowers on their respective plants, the smaller and even the more striking differences of the petals are apt to escape notice. These can be seen most clearly by removing a flower of each of the forms just named and spreading them out carefully on white paper. To do this best and to fasten them to the paper, a coat of mucilage is first applied. This allows the petals to be arranged without injury, and at once discloses their true size, form, and relation to each other.

In *O. Lamarckiana* the four large petals do not touch one another even at their nearest edges. Their narrowed bases leave wedge-shaped openings. The lobes of the petals are equal.

In *O. biennis* the form of the petals is at once seen to be different, and they do not touch each other. The petals do not run down to the base as straight lines, but curve in so as to leave a nearly flask-shaped opening. Furthermore, the petals are slightly unequally lobed, but always in one direction.

Laeta is very plainly different from *velutina* by the conspicuous and considerable overlapping of its four petals. These overlapped edges of the petals leave inclosed spaces at their base. These petals are also seen to be considerably larger than those of *velutina*.

The petals of *velutina* resemble those of *O. biennis* in general form, but are somewhat unequally lobed and larger. The spaces between the petals of *velutina* are larger and more nearly closed by the broad part of the petal than in *O. biennis*.

The cross-sections of the stamens mentioned in this paper were made as follows: Holes were made in cork with a small cork-borer, the anthers were placed carefully in them, and the holes were then filled with liquid glycerin jelly. After the glycerin had again become firm, the piece of cork with the specimens was placed in 96 per cent alcohol and allowed to dehydrate and further solidify the glycerin, which required two to three days. The sections were then made through both cork and specimens free-hand with a razor, and mounted for study in glycerin jelly. Such specimens, of course, can be made permanent by sealing the cover glass with Canada balsam.

Summary

1. The stigma of *Oenothera Lamarckiana* is much higher than the anthers. The anthers open both on rainy and sunny days, whereas some of the other forms open their anthers only on sunny days.

2. The European species, *O. biennis*, differs from the American species. Its anthers and stigma are of the same height, instead of being of different height as in *O. Lamarckiana*. Its petals, pubescence, and most of its cells are the smallest of any of the forms described, while those of *O. Lamarckiana* tend to be the largest.

3. The twin hybrids *laeta* and *velutina* show themselves by their foliage, flowers, the greater density and character of the pubescence in *velutina*, as well as the arrangement and form of the cells, to be distinct, and, in so far as has yet been investigated, constant forms.

4. On rainy days the anthers of the twin hybrids do not open, but only on sunny days, and then only part of them, whereas in all the other forms they open on both rainy and sunny days. This non-opening of the anther cells may probably be the beginning of sterility.

In conclusion I take pleasure in expressing my thanks to Professor DeVries for having placed at my disposal one of his laboratories and material from his garden for this investigation, and also for his many kind suggestions and assistance.

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AN EOCENE FLORA IN GEORGIA AND THE INDICATED PHYSICAL CONDITIONS[1]

EDWARD W. BERRY

(WITH TWO FIGURES)

Eocene plants have been thus far unknown along the Atlantic border, the most easterly known flora of this age having been that of the so-called Eolignitic of the Mississippi embayment, which while abundant is for the most part uncollected and undescribed. Contrasted with this paucity of eocene plants in the east, the western interior Eocene has a flora which in number of species probably exceeds the sum total of all the later tertiary floras of North America. There are also a number of eocene floras along the Pacific coast and in the far north as far as Alaska, the mouth of the Mackenzie River, and Greenland.

The following brief paper is concerned with a most interesting eocene flora of Claiborne age recently discovered, and studied by the writer in connection with the cooperative investigation of the coastal plain in charge of Dr. T. WAYLAND VAUGHAN of the U.S. Geological Survey. These notes partake of the nature of an abstract of this study, which will eventually be published in full by that organization.

The localities are all in eastern Georgia, where there is a marked transgression of the Claiborne sediments, burying all traces of Upper Cretaceous or earlier Eocene deposits and coming to rest upon beds of Lower Cretaceous age or even in some instances upon the crystalline rocks of the eastern Piedmont. The bulk of the plants come from the vicinity of Grovetown, about seventeen miles west of Augusta near the southeastern border of Columbia County. In this area the deposits, which consist for the most part of porous laminated light-colored clays alternating with heavy beds of sand, and more rarely beds of lignite, occupy a pre-Claiborne estuary eroded in the Lower Cretaceous and outcropping as a narrow tongue only two or three miles in width, and extending from the

[1] Published by permission of the Director of the U.S. Geological Survey.

main body of the Claiborne deposits in Richmond County in a northwesterly direction for a distance of about eighteen miles.

The plants are intimately associated with a few estuarine and shallow water marine invertebrates, such as *Modiolus*, *Ostrea*, *Nucula*, *Leda*, *Cytherea*, etc., which fully corroborate the age of the deposits derived from the study of the flora, where the data for correlation, in the absence of known Claiborne floras, consisted of comparisons with geographically remote floras like those of the Green River beds of Wyoming and those of the Paris basin and southern England. There are certain features, however, notably a marked indication of a rise in temperatures and increased humidity, which, in so far as they are known, characterize middle eocene floras everywhere. This is known to be the case in America, it is markedly shown in the floras of England and France, and is emphasized in the numerous late eocene floras from a large number of arctic localities.

Among the forms collected from the Georgia Eocene are new species of *Acrostichum*, *Arundo*, *Castanea*, *Conocarpus*, *Dodonaea*, *Ficus*, *Malapoenna*, *Momisia*, *Pisonia*, *Potamogeton*, *Rhizophora*, *Sapindus*, *Terminalia*, and *Thrinax*, including the first fossil occurrence of species of *Conocarpus*, *Momisia*, and *Thrinax*.

The foregoing forms represent twelve families and include one fern, three monocotyledons, and ten dicotyledons. No gymnosperms, which are usually represented in European Lutetien floras by at least the genus *Podocarpus*, have been discovered. It will be observed that only two forms, the *Castanea* and the *Potamogeton*, are not coastal forms, and the latter is an aquatic whose presence associated with coastal swamp or strand plants is not difficult to explain. The *Castanea* then apparently represents the only upland type preserved in this flora, and as it is not common, the presumption is strong that it was brought down to the basin of sedimentation by some eocene river, most likely by the river which originally occupied the trough of the subsequent estuary.

Turning to the remaining twelve species, we may enumerate with profit their closest allies in the existing flora. The *Acrostichum* is represented by *A. aureum* Linn., the *Arundo* by *A. Donax* Linn., the *Conocarpus* by *C. erectus* Linn., the *Dodonaea* by *D. viscosa* Linn.,

the *Ficus* by various tropical American figs, the *Malapoenna* by *M. geniculata* (Walt.) Coulter, the *Momisia* by *M. aculeata* (Sw.) Kl., the *Pisonia* by *P. macranocarpa* Donnell Smith, the *Rhizophora* by *R. Mangle* Linn., the *Sapindus* by *S. saponaria* Linn., the *Terminalia* by *T. phaeocarpa* Eichler, and the *Thrinax* by various West Indian species of that genus.

When we consider the habitat of these modern forms and that of their allies, we find that they inhabit the tidal nipa swamps of the orient, the mangrove swamps of the orient and the occident, the beach jungle of the strand, or the landward side of coastal sand dunes in the tropics. Nearly every one of the fossil species is represented by forms found in the existing flora of the Florida keys or along the shores of peninsular Florida, some like *Conocarpus* flourishing equally well on either muddy or sandy shores. Every species (except *Castanea*) is represented in the American tropics, and four of these existing representatives (*Conocarpus*, *Dodonaea*, *Rhizophora*, and *Sapindus*) range northward to Bermuda in the path of the gulf stream. In looking over SCHIMPER's classical *Indo-malayan strand flora*, the following forms, which are strictly comparable to the Georgia eocene plants, were noted as being more or less prominent elements in the oriental strand flora: *Acrostichum* (*Chrysodium*, 1 sp.), *Dodonaea* (1 sp.), *Eugenia* (2 species which are represented in the west African and American tropics by the allied genus *Conocarpus*), *Ficus* (1 sp.), *Malapoenna* (*Litsaea*, 1 sp.), *Pisonia* (4 sp.), *Rhizophora* (2 sp.), *Sapindus* (1 sp.), and *Terminalia* (1 sp.). Of these forms the *Sapindus*, *Terminalia*, *Dodonaea*, *Ficus*, *Malapoenna*, and *Pisonia* are more particularly elements of the littoral forest (beach jungle of KURZ, *Barringtonia* formation of SCHIMPER), while the others are integral members or rather intimately associated with the mangrove or the nipa associations. It is really remarkable to what an extent the identified elements in the Claiborne flora corroborate one another and definitely denote the character of their habitats, which were, on the one hand, mangrove swamps at certain points where the conditions were favorable, and elsewhere the vegetation of the rain forest which clothed the sandy beaches or was developed behind dunes, which possibly formed the highest inner margin of the beach in places.

Certain rather definite climatic deductions appear to be justifiable from the foregoing facts. None of the modern representatives of this eocene strand flora flourish north of the winter isotherm of about 50° F., and the majority do not occur north of the winter isotherm of 60° F. None of the fossil forms, except possibly the *Potamogeton*, the modern species of which range over a great many degrees of latitude, or the *Castanea*, which likewise has a wide range, would be expected to occur outside of the areas where the modern subtropical rain forests are developed. We would expect the Claiborne climate in the area under discussion, at least at low elevations along the coast and in proximity to the eocene gulf stream, to have been uniformly humid with an abundant and evenly distributed rainfall. The temperature would have been uniform, not necessarily extremely hot, and any degree of winter cold would have been fatal.

These considerations are in a large measure corroborated by what we find to have been the conditions in Europe at this time. It is well known that the middle eocene floras of Europe show many tropical characters absent in the earlier Eocene. These first become marked in the fruits from the London clays and the leaves from Alum Bay and in homotaxial deposits on the continent, and while it was once the fashion to see Australian affinities in these floras, they show closer affinities with the modern floras of Malaysia and tropical America. The accompanying sketch map (fig. 1) will bring this out very well. It shows the area of distribution of the modern genus *Nipa* and the eocene genus *Nipadites*, which is indistinguishable from the modern *Nipa*. The latter has a single species inhabiting the tidal waters of the Indian Ocean, ranging from India through the Malay Archipelago to the Philippines, and vying with the mangroves for possession of the tidal flats. It produces clusters of large floating fruits, and it is exactly similar in both form and structure to the fossil fruits which form the basis for the genus *Nipadites*. As the map shows, these tropical or subtropical floras ranged northward in Europe at this time to southern England, or to about the latitude of Newfoundland on this continent, and these eocene *Nipa* swamps furnished a congenial habitat for one or more species of *Acrostichum* closely allied to that

of Georgia, and other forms are not wanting. In the Paris basin a species of *Pandanus* is associated with the *Nipadites*, while at Bournemouth *Gleichenia* and various tropical Polypodiaceae occur. The Lutetien stage of the Eocene in Europe and the Claiborne stage in America are both characterized by a remarkable transgression of the sea, the approximate shore line of the Claiborne sea being shown on the accompanying map (fig. 2). This map makes no pretence to exactness, which would be impossible on so small

FIG. 1.—Sketch map showing geographical distribution of the existing genus *Nipa* Thunberg and the eocene genus *Nipadites* Bowerbank; horizontally lined area shows single existing species; vertically lined area shows eocene species.

a scale map, even if the areal extent of the Claiborne deposits were accurately known. What it is intended to illustrate is the relation of land to sea and the line of advance of the flora which was necessarily along the shore from equatorial America, where undoubtedly the representatives of this flora flourished during the whole of the Tertiary.

In studying the Georgia flora, the writer became much interested in the means of dissemination of its modern allies, which in so far as they are known are worthy of enumeration. It has been shown that certain species of *Eugenia*, *Terminalia*, *Rhizophora*.

Pisonia, and *Sapindus* have become adapted for dispersal through the agency of ocean currents, by specialization of their fruits or seeds, which have developed air chambers or woody husks for buoyancy, and practically impervious seed coverings for the exclusion of sea water from their vital parts. Everyone is familiar

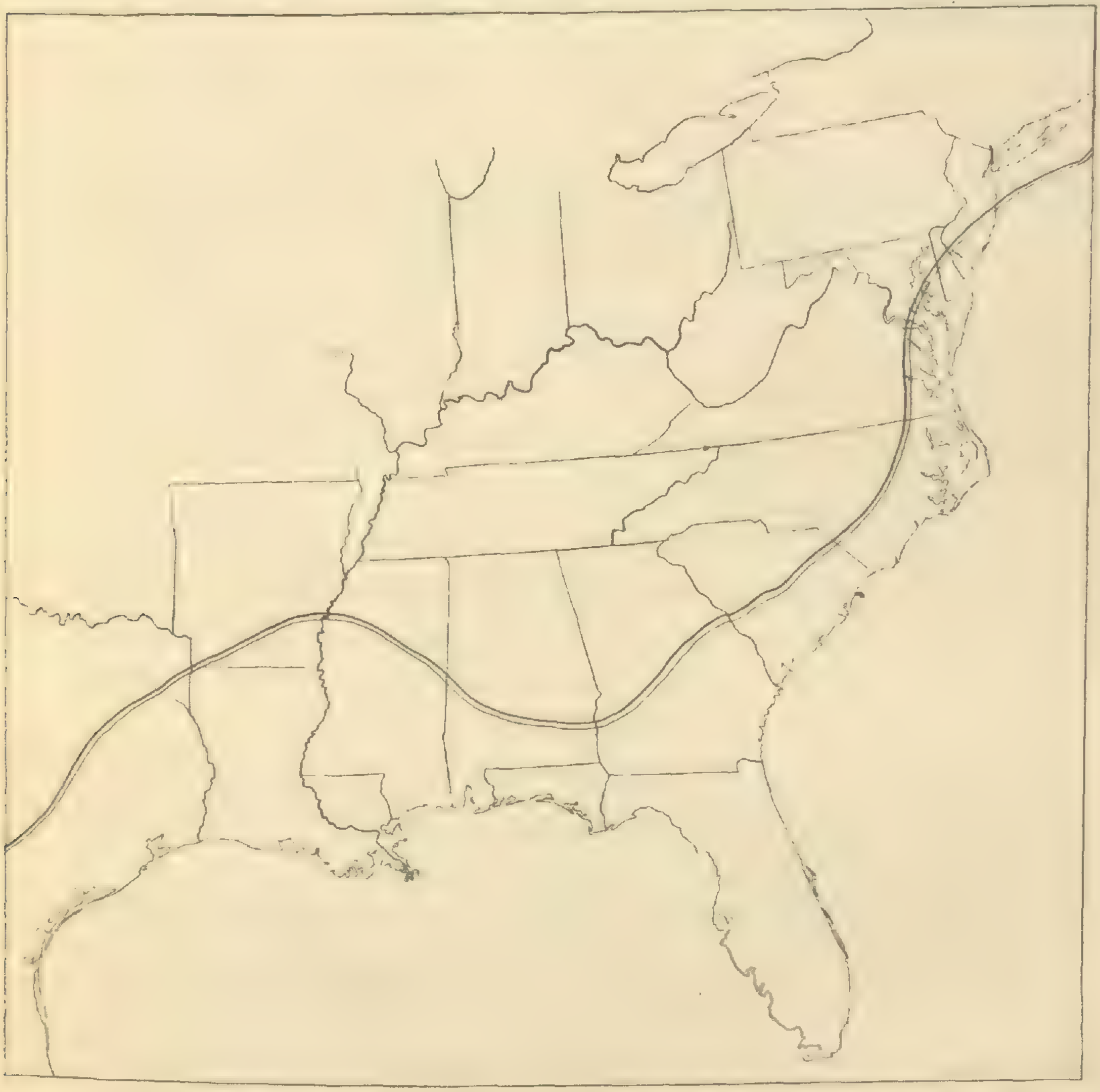

FIG. 2.—Sketch map showing the approximate shore line of the middle eocene sea in southeastern North America.

with the extreme specialization of the mangrove, which sends its germinating plantlets out into the world fully prepared to anchor themselves in water of the required depth, but the comparable specializations of the other members of these floras, though less in degree, are almost as effective, judging by the present geographical distribution of these genera, so that ocean currents must play a considerable rôle in distribution, despite the contrary opinion of DE

CANDOLLE. Other members of the Claiborne flora may be supposed to have been distributed by fruit-eating birds. This seems clearly to apply to *Ficus* and probably to *Malapoenna*.

It can be readily shown that the existing flora of peninsular Florida, the Bahamas, Bermuda, etc., contains a large element which has been derived in comparatively recent geological times from the south. In the case of the Bahamas and Bermuda, almost their entire flora has had such an origin. If, however, we study geographical distribution in the light of historical geology, we find that the main elements of these modern floras were already in existence in the Middle Eocene, if not earlier. Experience teaches us that nearly all modern plant families, unless it be the most specialized forms like the orchids among the monocotyledons or the composites and their allies among the dicotyledons, were at some time more widely distributed than they are at present, and that the details of modern geographical distribution represent in a less degree the interchange of types between different areas than they do the greater or less degree of segregation of descendants of forms once spread over much wider areas. Uniformity appears to have been the rule during geologic history and not the exception.

From a study of the Claiborne flora it is evident that the main elements of the modern flora of tropical America reached as far northward in the Eocene as latitude 33 and probably much farther, and that in post-Eocene time they retreated southward. DALL,[1] from a study of the tertiary faunas of Florida, places a marked change in climate at the close of the Oligocene, and accounts for it by the elevation in the Florida area and the shifting to the eastward of the gulf stream with an inshore southerly flowing cold current.

Thus while the strictly modern movement of the subtropical flora along the course of the gulf stream has been from the south northward as the various coral islands of the Bahamas became evolved, this dispersion was preceded by a similar spread of the tropical flora on a much more extended scale during the early Tertiary.

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[1] DALL, Trans. Wagner Inst. 3:1549, 1550. 1903.

NOTES ON THE SEX OF THE GAMETOPHYTE OF ONOCLEA STRUTHIOPTERIS

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During the past two or three years the writer has been collecting data from a study upon the gametophyte of *Onoclea Struthiopteris* with reference especially to the dioecious character of the prothallia, and while this study is in no way completed, it has been deemed advisable to make public some of the facts observed, inasmuch as the data obtained supplement those set forth in a very interesting paper, appearing in a recent number of this journal, by Miss WUIST.[1]

The impression is general that the prothallia of *Onoclea Struthiopteris* are dioecious,[2] and although this is generally true, it is not strictly so, as bisexual prothallia may readily be found under ordinary and perhaps optimum cultural conditions. In 1907, in an address before the Indiana Academy of Science,[3] I made the following statement:

> The writer has recently begun the study of a fern, whose prothallia have been reported as strictly dioecious, and if the spores of the same are well nourished, female prothallia will predominate, while with poor nourishment the vast majority of spores will give rise to male gametophytes. An examination of cultures grown under favorable conditions for laboratory use, in which the spores were sown thickly, showed that certain spores produced strictly male plants, others female, and still others bisexual prothallia. A small number of spores were isolated and grown under similar and very favorable conditions, with similar results. The pure males were almost equal in number to those bearing the female organs, while the bisexual plants were few, being about 4 per cent of the whole number. The foregoing results seem to lend encouragement to the view that environmental conditions may have much less to do with the development of male and female prothallia than had hitherto been supposed. The very brief study showed clearly that in the fern in question

[1] WUIST, ELIZABETH DOROTHY, The physiological conditions for the development of monoecious prothallia in *Onoclea Struthiopteris*. BOT. GAZETTE **49**:216–219. 1910.

[2] CAMPBELL, D. H., Mosses and ferns. Edition 2, p. 314. 1905.

[3] MOTTIER, D. M., History and control of sex. Proc. Ind. Acad. Sci. 1907. pp. 44–45.

there is a great mortality among the spores, which, as can be readily seen, vary greatly in size. Among the first things to establish in this and similar cases, is whether mortality is greatest among the smaller or larger spores, and whether the prothallia springing from the smaller spores tend to remain small and produce only antheridia, while the larger female plants arise only from the larger spores, and so on.

The fern in question was *Onoclea Struthiopteris*, although the name of the plant was not stated in the address in question.

Miss WUIST (*op. cit.* p. 217) states that about 1 per cent of the prothallia of soil cultures were monoecious. This estimate seems to me to be much too low, inasmuch as an examination of a larger number of prothallia, since the publication of the paragraph just quoted, showed that about 12 per cent were monoecious. The prothallia from which this estimate was made were grown upon soil under good cultural conditions. The plants, although grown thickly, were vigorous, normal in every way, and in fact the cultures seemed to leave nothing to be desired. The monoecious prothallia were as a rule young, bearing one to several archegonia, and were 1.5–3 mm. in diameter. Antheridia were very rarely found on older and larger prothallia, although little attention was paid to exact size and measurement. The antheridia were as a rule upon the ventral side, among or near the rhizoids, hence upon the older tissue; very rarely did they appear at the margin of the prothallium. In one case an antheridium was found upon the archegonial meristem.

In determining whether prothallia were monoecious, I did not rely at all upon an examination of fresh material, but all plants were carefully fixed, stained *in toto* with borax carmine, cleared, and examined in clove oil or balsam. In this way a single small antheridium could easily be found upon a prothallium, and cases were not infrequent of a single antheridium appearing inconspicuously among the rhizoids. It has been my experience that one or two immature antheridia among the rhizoids are easily overlooked when the plants are examined alive. In material thus stained and cleared, one may also more readily and accurately detect very small male plants adhering among the rhizoids of the larger prothallia bearing archegonia.

In order to ascertain whether crowding was in any way respon-

sible for the sex of the gametophytes, cultures were made by sowing spores thinly upon the soil and keeping the cultures under the most favorable conditions available. One such culture may be mentioned in detail. In this 207 spores were sown and 150 prothallia harvested. Of these 78 were pure males, while 72 bore archegonia, and of the latter 10 per cent were monoecious. Cultures were also made to determine, if possible, whether the spores of any given sporangium were male or female, as has been reported for certain liverworts. In this set of experiments the spores of individual sporangia were sown upon earth in separate dishes, with results similar to those from spores sown from many sporangia, that is, both male and female prothallia were grown; of the female, those bearing archegonia, some few were bisexual. Such experiments show conclusively that sporangia do not bear spores giving rise exclusively to male or female prothallia, and the fact that prothallia are bisexual is proof that no sex-differentiating chromosome is present in this fern.

No effort has been made up to this time by the writer to induce the development of antheridia upon "female" prothallia. Interesting experiments along this line have been carried out by Miss WUIST, as mentioned in the foregoing, with the following results: monoecious prothallia were obtained by transferring the plants from distilled water to Knop's solution, in which they were further cultivated; by transferring "female" prothallia from soil to a nutritive solution, and by transferring from one nutritive solution to another.

These experiments indicate that gametophytes bearing archegonia only may be induced to develop antheridia as a response to environmental conditions. Knowing that dioecism has not been completely established, these results, though important, are not surprising. They do not show a very far-reaching influence of environmental factors in regard to the regulation of the development of sex cells; for I have frequently observed in older cultures, that is, about five months after sowing, that certain "female" prothallia, in which an egg failed to be fertilized, developed from the oldest parts numerous small lobes which give that end of the prothallium a finely fringed appearance, and upon these lobes

numerous antheridia were produced. Such prothallia were well nourished, with a deep-green color, and continued to develop the archegonial meristem, which produced continuously numerous archegonia. The specimens before me at this writing are 5–6 mm. in length. As stated, the antheridial lobes were confined generally to the posterior or older parts of the prothallia, but they may extend a short distance forward along the margins. Antheridia were not observed, except in very rare cases, upon the archegonial meristem.

After all, the fact that archegonial plants may develop organs of the opposite sex, either normally or in response to conditions controlled in a measure by the experimenter, may readily find a satisfactory explanation, but the case may be different in regard to the prothallium that produces only antheridia. If purely male prothallia of *Onoclea Struthiopteris* are merely those that do not become large enough, because of nourishment, to bear archegonia, why is it that these pure males cannot be made to grow large enough to develop the female organ? The writer knows of no case on record in which this has been done. If the male plants could be made to develop the archegonial meristem and its archegonia, then it may be said that the environment (which of coures means chiefly nutrition) controls sex to that degree. The writer has not been able to believe that male prothallia of the fern in question are merely those that do not become large enough to bear archegonia, but that certain spores are predetermined to develop into purely antheridial plants, and others into those capable of forming archegonia. If there were a sex-determining chromosome, then one half of the spores would be male and one half female, but as the "female" prothallia bear occasionally antheridia, it cannot be said that a sex-determining chromosome is present. The explanation which we are able to give at present is that in certain spores the male tendency is dominant, while in others it is the female, but such statements mean little at present.

In a foregoing paragraph reference was made to the mortality among the spores, and to the variation in their size and apparent vigor. Some are larger and more healthy looking than others, and, as in many plants, many spores seem to be and doubtless are

abortive. It was thought at one time in this study that the smaller spores were the ones that produced the purely antheridial prothallia, but sowings were made by selecting, in so far as possible, the more vigorous spores (an extremely tedious process), but the results did not bear out the expectation. Owing to the difficulties of selecting individual spores, it is not maintained that the last-named experiment is of any great value, at least the writer does not lay any stress upon the results. It seems reasonable that a larger percentage of the smaller spores, that is, those which show less chlorophyll and which germinate less readily, would fail to grow than in the case of the larger ones, so that the possibility of the smaller and abortive-looking spores producing chiefly male prothallia is not excluded. However, on this point the writer can make no definite assertions.

The foregoing statements may be summarized as follows:

1. The spores of *Onoclea Struthiopteris* when grown upon earth, under optimum cultural conditions, produce regularly three kinds of prothallia: small plants bearing only antheridia, the so-called male gametophytes; larger prothallia bearing only archegonia, the female gametophytes; and those bearing both archegonia and antheridia, the bisexual or monoecious prothallia.

2. Archegonial prothallia, which continue growth without bearing a sporophyte, sometimes develop numerous small lobes from the older portions, upon which numerous antheridia appear.

3. The gametophyte, therefore, is not strictly dioecious, and there is in all probability no sex-determining chromosome.

4. It is highly probable that the development of purely male or female gametophytes is not dependent upon conditions of nutrition, but that the sexual tendency is predetermined in the spore. Environmental conditions, or the failure of an egg to give rise to a sporophyte, owing to a lack of fecundation, may induce the development of antheridia upon archegonial plants, which continue their growth for some months.

5. Pure males result, in so far as is known, under good cultural conditions from the dominance of the male tendency in the spore over the female tendency.

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BRIEFER ARTICLES

AN ATMOGRAPH

(WITH FOUR FIGURES)

The introduction of the porous cup atmometer by LIVINGSTON has been followed by great activity in securing evaporation data in relation to plant life. Readings have usually been made with reference to a zero point, usually a file-scratch, on the wall of the reservoir containing the water. For most workers it has been impossible to visit the field more frequently than once a week. The records secured were of course simply the total weekly evaporation.

It is becoming increasingly clear that the record of total weekly evaporation can be evaluated only when we know the rate of evaporation at all times, and particularly when we know the maximum and minimum rate. This need can be met only by some form of automatic measuring and recording device. No such instrument has yet come into general use. To meet the conditions of the work such an instrument must measure in convenient units and record in graphic form. It must be so simple that it may be set up easily in the field and trusted to work with only occasional attention. Also the cost of construction must not be so great as to prohibit the employment of a sufficient number of them to secure comparative data. In attempting to meet these conditions as I have found them in the field, the instrument described herewith has been designed (fig. 1).

The device (fig. 2) consists essentially of an oscillating beam (*A*), which may be caused to tilt by the movement of mercury in a tube (*B*) and its connected bulbs, advantage being taken of the oscillation to open the stopcock (*C*) and to close it again. At the same time an electric circuit is closed which actuates the pen of the chronograph.

In practice the whole apparatus is filled with water and the stopcock closed. Mercury is poured into the bulb b', nearly filling it, the inlet e' is connected with the supply tank of water, and the outlet at d' with the atmometer. The water which evaporates from the atmometer is replaced by a flow through the pipes *d*, *c*, and *a* from the supply in the bulb b'. The mercury in *b* follows the water, partially filling b'.

Whenever the transfer of weight from *b* to b' has gone far enough to shift the center of gravity to the right of the center of suspension

(*F*), the beam *A* is caused to revolve until checked by the stop *g'*. As the end of *A* moves upward it carries with it the flange *f*, which strikes the

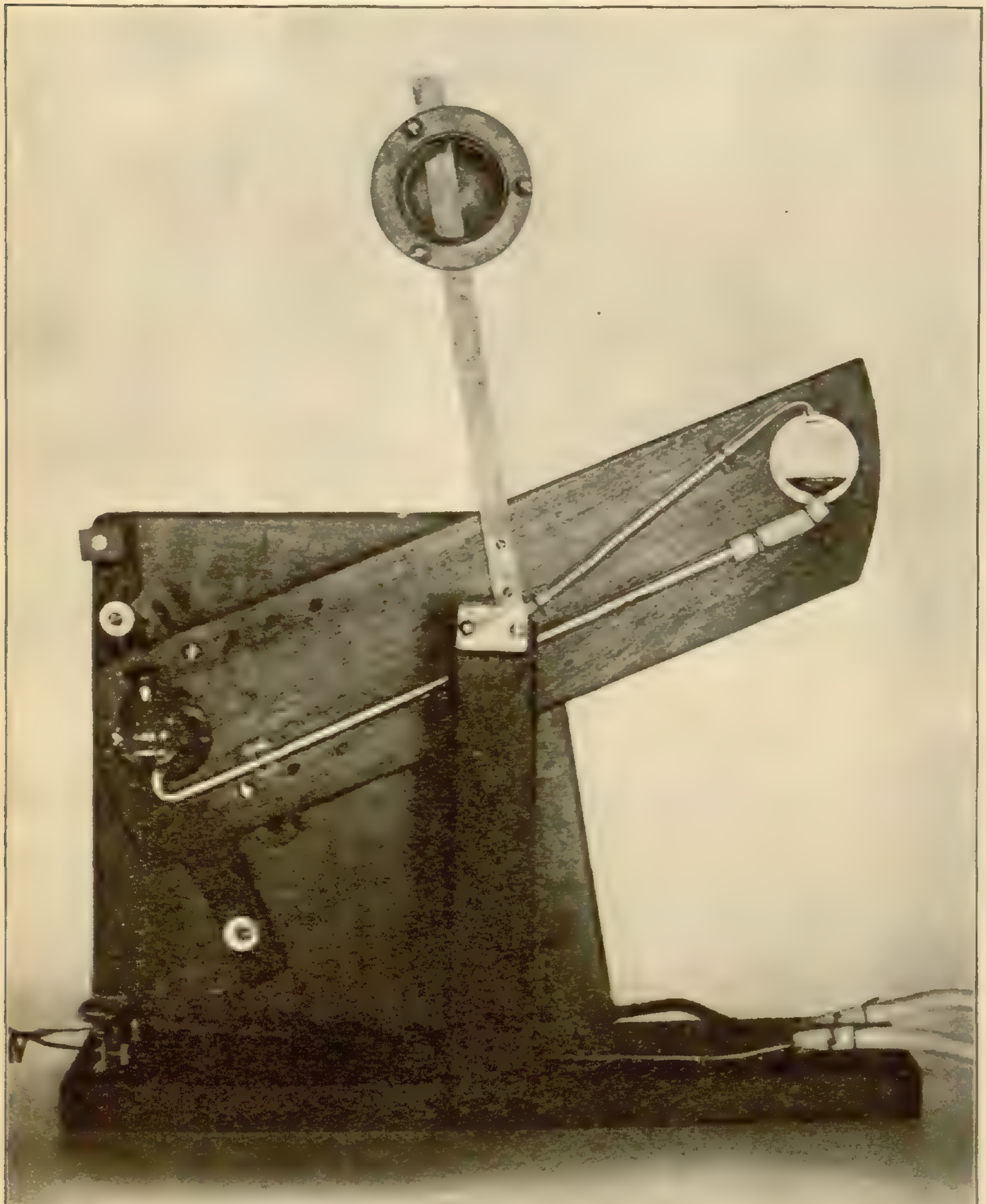

FIG. 1

handle of the stopcock and pushes it upward, thus opening the passage from the water supply through *e*, *c*, and *a* into *b'*. The stop *g'* is so located that *b* does not rise to quite so high a level as *b'*, and the mercury

therefore flows back toward *b*, followed by the water which again fills *b'*. The shifting of weight toward the left causes *A* to return to its

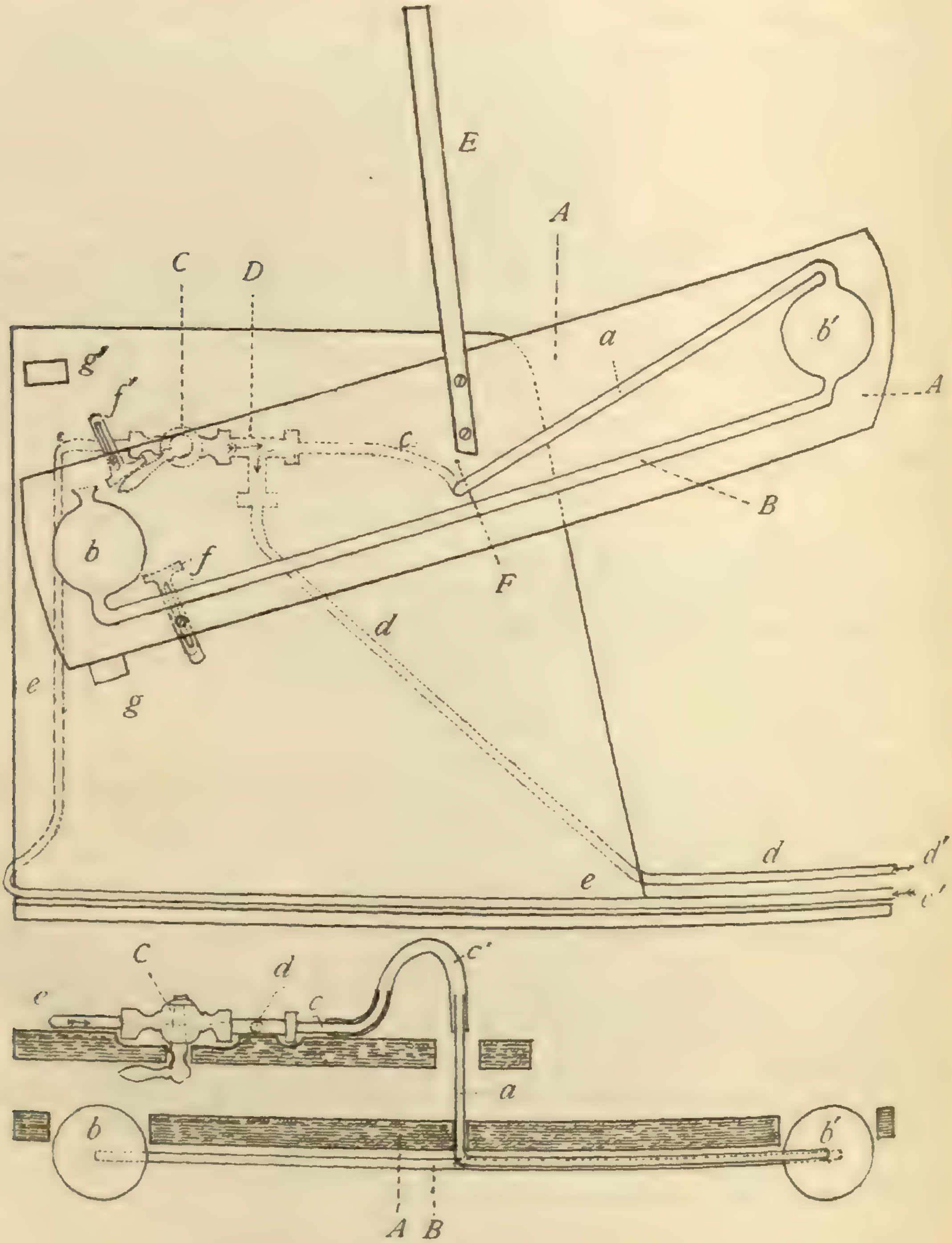

FIG. 2

former position, the flange *f'* in its downward movement closing the stopcock *C*.

The point of suspension (*F*) is placed lower than the center of gravity

of the whole system consisting of A and its attached parts. In the initial position, as shown in the figures, the center of gravity is not only higher than F, but also at some distance to the left of a perpendicular through F. A considerable amount of mercury must therefore pass into b' before the center of gravity will have shifted to the right of the perpendicular sufficiently to tilt the beam. The tilting of the beam carries the center of gravity yet farther to the right, and the beam therefore rests in the new position until the reverse movement of the mercury has carried the center of gravity to its former position in the beam. It is evident that if the center of gravity be raised yet higher above F, it will also be farther to the left when in the first position, and a larger volume

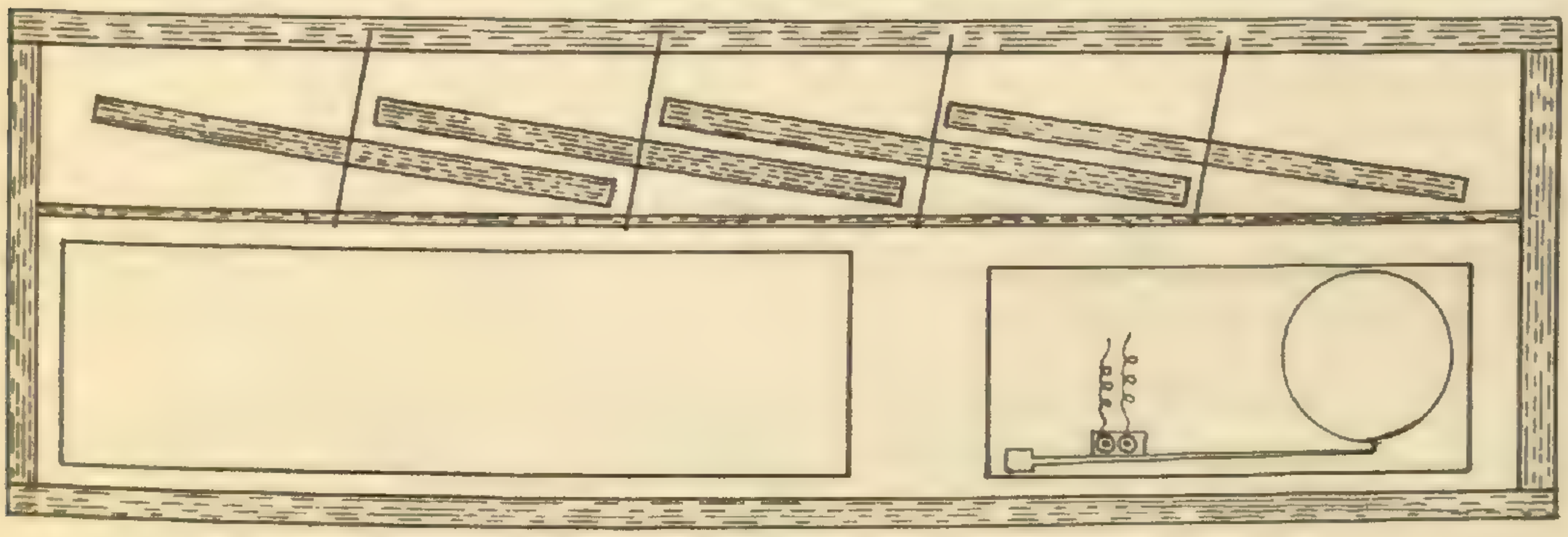

FIG. 3

of water will have to be displaced from b' by mercury before the beam will tilt. Each record, therefore, will indicate a larger amount of water.

Advantage is taken of the relation between the center of gravity and the center of suspension to calibrate the instrument. A weight is placed upon the bar E, and by sliding it up or down the bar or exchanging it for another, the center of gravity is adjusted at will. The point of suspension may also be moved.

The atmograph, set up as shown in the photograph (fig. 4), recorded the passage of 10 cc. units. By lowering the weight, the quantity could be reduced by half, or set at any intervening amount. Experience indicates that under ordinary conditions 10 cc. will be a convenient unit for field work with LIVINGSTON atmometers.

Standard copper pipe and fittings are used throughout, no rubber being employed excepting for the flexible connection c'. Electrical connections are made from one of the binding posts shown in the photograph to the pipe e, and from the other to the flange f. The circuit is closed through the stopcock while f is in contact with the handle. A single dry cell is employed as the source of current.

The atmograph may be employed in the measurement of the transpiration of an excised branch by tying the branch into a rubber tube and connecting with the outlet at d', or it may be used in other cases in which it is desired to measure the passage of water.

For observation in the field the instrument must be inclosed in a box in order to preserve it from interference. If it is desirable to operate several atmometers at a single station, as described by YAPP, the atmographs may be compactly arranged in a box with a common reservoir

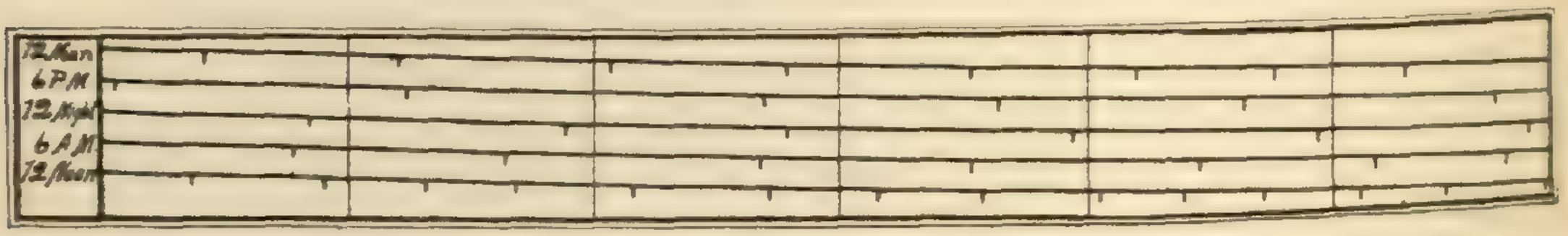

FIG. 4

and a single chronograph (fig. 3), as many pens being used as atmographs. Experience has shown that the piping leading to the atmometers should be metallic. Glass and rubber are subject to many hazards, not only from vandals but also from the less conspicuous members of the fauna. Grasshoppers sometimes exhibit a very interesting, but none the less disastrous, adaptation of appetite to the supply of rubber tubing.

For a series of simultaneous records a chronograph drum rotating in seven days will be found desirable. The records shown in fig. 4 were made in the laboratory upon a chronograph rotating once in six hours and with a group of four LIVINGSTON atmometers. The interval required for the evaporation of 10 cc. by the four cups has been noted to vary, within twelve hours, from a maximum of 113 minutes to a minimum of 17 minutes.—W. L. EIKENBERRY, *The University of Chicago*.

THE SPORANGIUM OF LYCOPODIUM PITHYOIDES

(WITH PLATE VII)

So much importance has been attached at various times to the position, shape, and development of the sporangium in *Lycopodium*, that any unusual forms are of interest. The rare species *L. pithyoides* Schlect and Cham., which is figured in a former paper,[1] presents certain variations. The stem tip is large and blunt, with a flattened apical region. The earliest stages in the development of the sporangium agree with those of previously

[1] STOKEY, A. G., The roots of *Lycopodium pithyoides*. BOT. GAZETTE **44**:57–63. 1907.

described species (fig. 6). The leaves appear in close succession on the flattened tip, leaving no evident internodal region. The development of the internode afterward is very rapid, causing a conspicuous shifting of the position of the sporangium (fig. 7). The rapid growth of the internode, combined with the unequal rate of growth of the two sides of the sporangium, causes the foliar structure to become axial. A change of position to this extent is not uncommon in other species of *Lycopodium*, but in *L. pithyoides* there is a continued inequality in the rate of growth, so that the sporangium eventually takes a position on the stem entirely distinct from the leaf. At maturity the sporangium is not disturbed if the leaves are pulled off. The development in this case is the reverse of that in most species of *Selaginella*, in which the sporangium arises as a cauline structure, but becomes foliar when mature; while in *L. pithyoides* it is foliar in origin, but cauline at maturity.

The sporangia of *L. pithyoides* are very large, attaining a breadth of 2–2.5 mm., and resemble those of *L. dichotomum* Jacq., according to BOWER's description and comparison,[2] although Miss SYKES's drawing,[3] while suggesting a tendency in the sporangium to be cauline, does not indicate a very close resemblance in other points. The stalk is short and relatively slender, ranging from 12 to 18 cells in diameter in sections cut radially, and about twice that in the other diameter. The cells are elongated and thin-walled, with no corner thickening and no trace of lignification such as Miss SYKES has described in *L. clavatum* and other species. The vascular strand of the leaf shows no tendency to approach the sporangium. The leaf trace arises from the vascular cylinder 5–6 mm. below the sporangium, turning sharply upward and then making an outward bend as it approaches the leaf.

The sporangia resemble those of *L. dichotomum* in the number of wall layers also. In the upper part of the sporangium there are usually four layers, but there may be even more owing to the irregularity in the arrangement of the middle layers (fig. 4). At the base of the sporangium the wall may consist of 6–8 layers. In a young sporangium (fig. 8) the order of division and the relation of the layers is very plainly seen, but in the older sporangia this regularity of arrangement is lost. The inner layer or tapetum is well defined as a dense, darkly staining layer. The tapetal cells do not show any tendency to become rounded on the inner face. In

[2] BOWER, F. O., Studies in the morphology of spore-producing members; Equisetineae and Lycopodineae. Phil. Trans. Roy. Soc. London B **185**:516. 1894.

[3] SYKES, M. G., Notes on the morphology of the sporangium-bearing organs of the Lycopodiaceae. New Phytologist **7**:41–60. 1908.

some almost mature sporangia the tapetum is alive, while in others very little older the tapetum is entirely empty, but granules and droplets are abundant along its inner face. The emptying process is apparently a rapid one, as a considerable number of sporangia were found in both conditions but none in any intermediate stages. The cells of the tapetum retain their shape for a considerable time and do not become crushed and flattened until much later. The subarchesporial pod is well developed (fig. 2) and slightly irregular in outline, but does not form processes in the sporangium.

The leaves afford little protection to the sporangia except in the very early stages, owing to the fact that they are relatively narrow (figs. 3, 5) and soon become recurved. The line of dehiscence, which is marked by smaller cells than the rest of the wall, is median (figs. 1, 3).—ALMA G. STOKEY, *Mt. Holyoke College, South Hadley, Mass.*

EXPLANATION OF PLATE VII

FIG. 1.—Longitudinal section of sporangium. ×28.

FIG. 2.—Tangential section of a sporangium. ×26.

FIG. 3.—Transverse section through base of sporangium and sporangium stalk. ×28.

FIG. 4.—Section of part of the wall of sporangium. ×345.

FIG. 5.—Transverse section of sporangium. ×28.

FIG. 6.—Longitudinal section through leaf, showing one of the initial cells of the sporangium. ×725.

FIG. 7.—Longitudinal section through stem tip, showing three stages in development of sporangia. ×36.

FIG. 8.—Longitudinal section of young sporangium, showing origin of wall layers ×345.

THE BOTANICAL CONGRESS AT BRUSSELS

The Third International Botanical Congress was held at Brussels, Belgium, May 14–22, 1910. Saturday, the 14th, was the day for registration. On Sunday, the 15th, the members of the congress assisted at a session of the Royal Botanical Society of Belgium held in the "dome" of the large building connected with the Jardin Botanique, at which several interesting papers were presented by the members of the society. Two of the general sessions of the congress were held in the same room, the opening session on Monday morning the 16th, and the closing one on Sunday the 22d. No regular sessions of the congress were held in the evenings, but during the week several interesting papers on phytogeographical subjects, economic botany, etc., were given in the evening.

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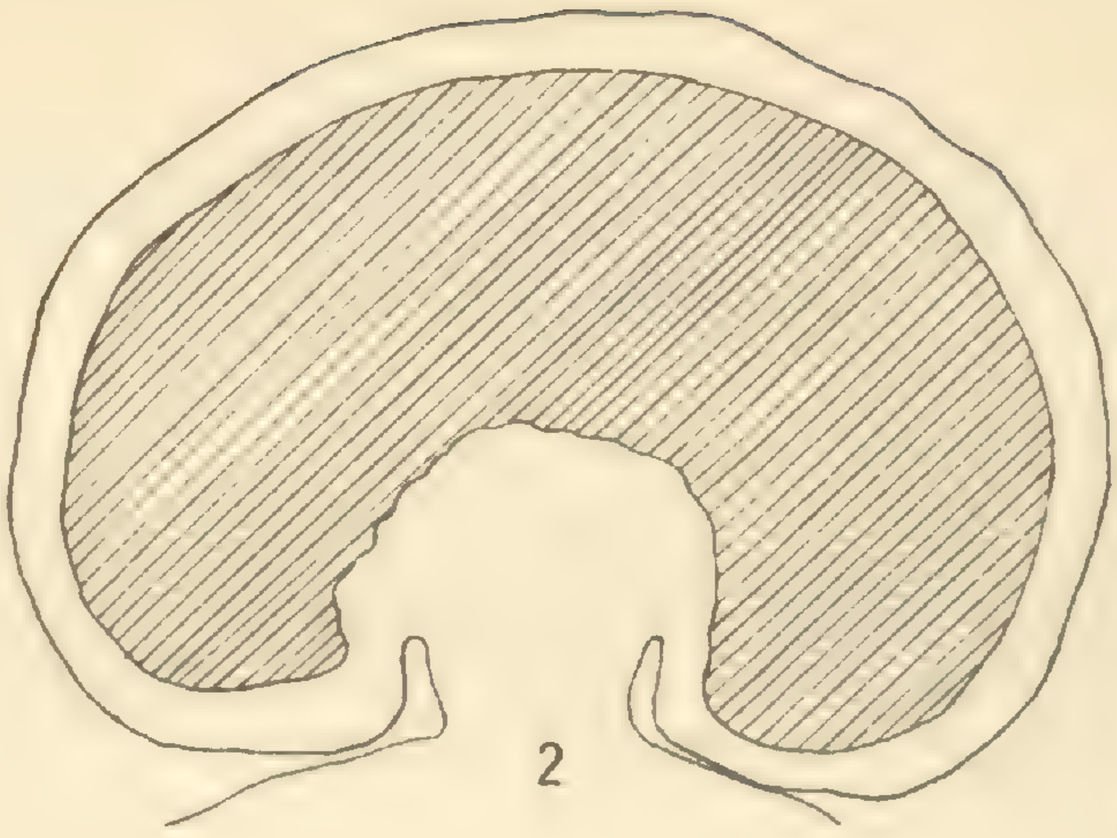

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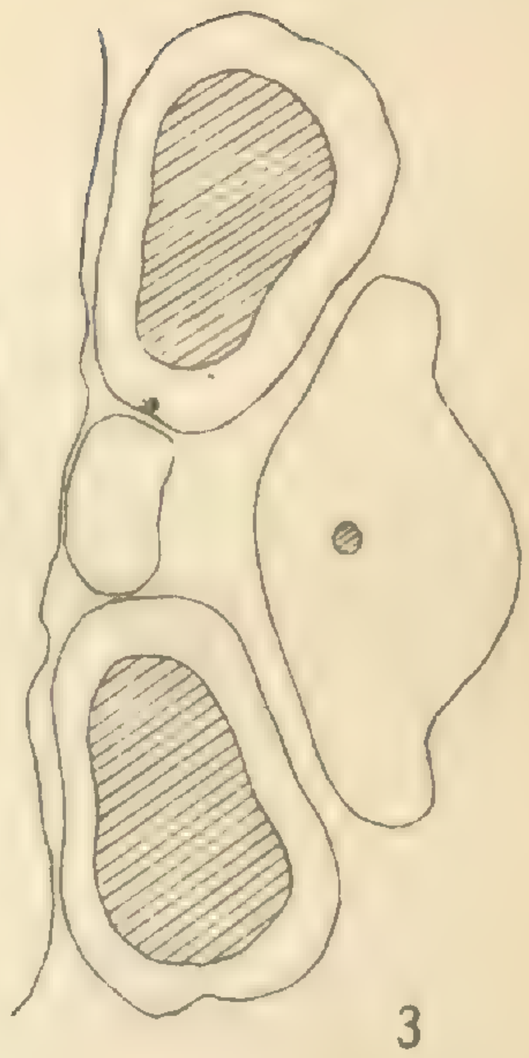

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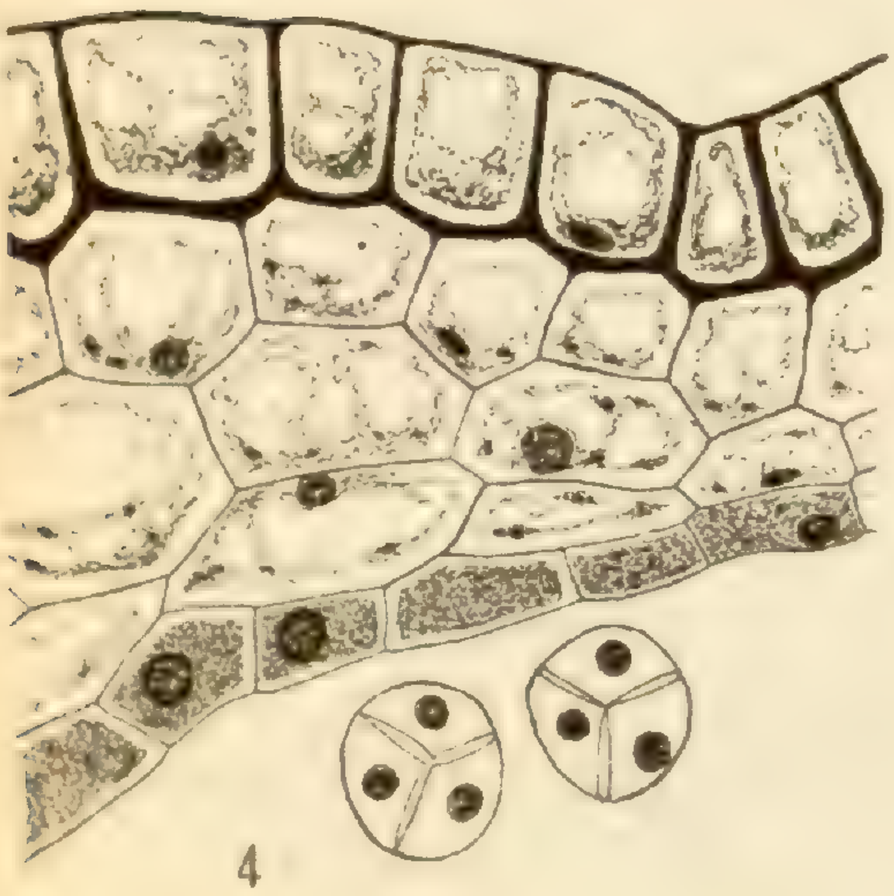

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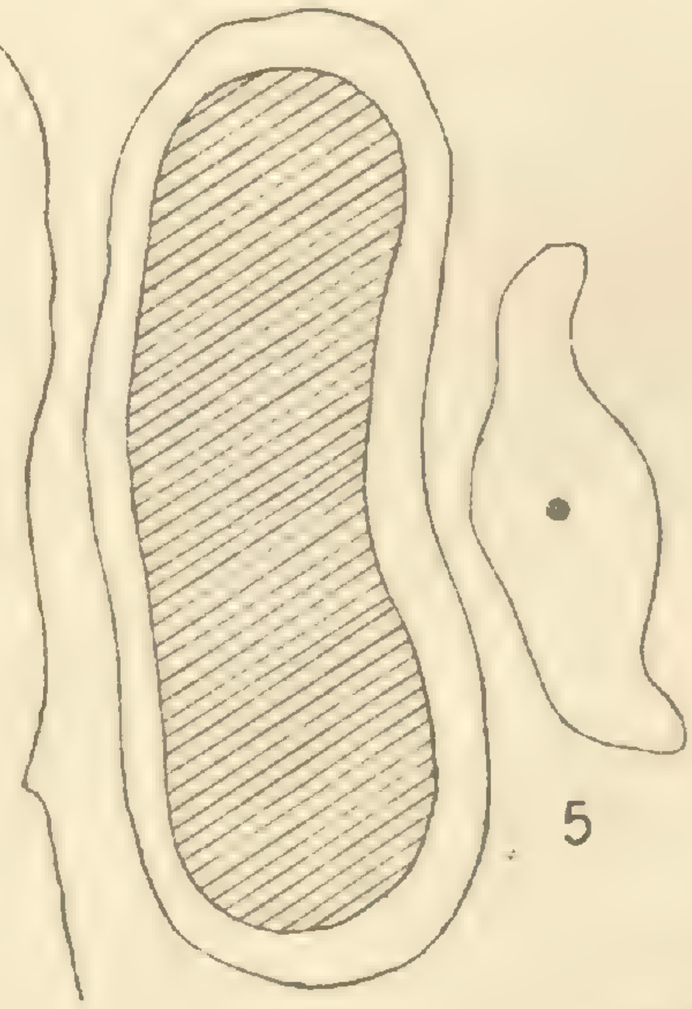

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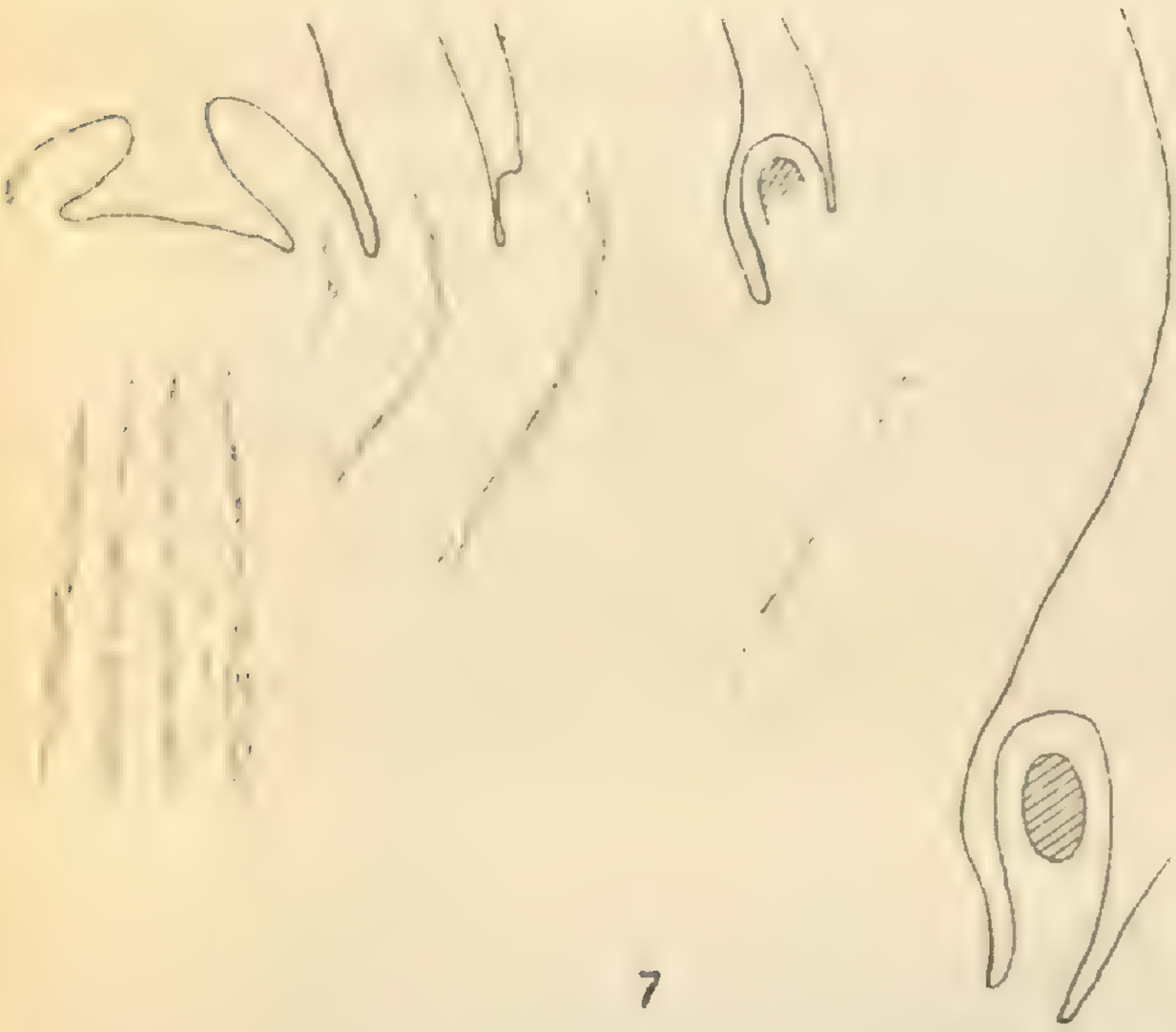

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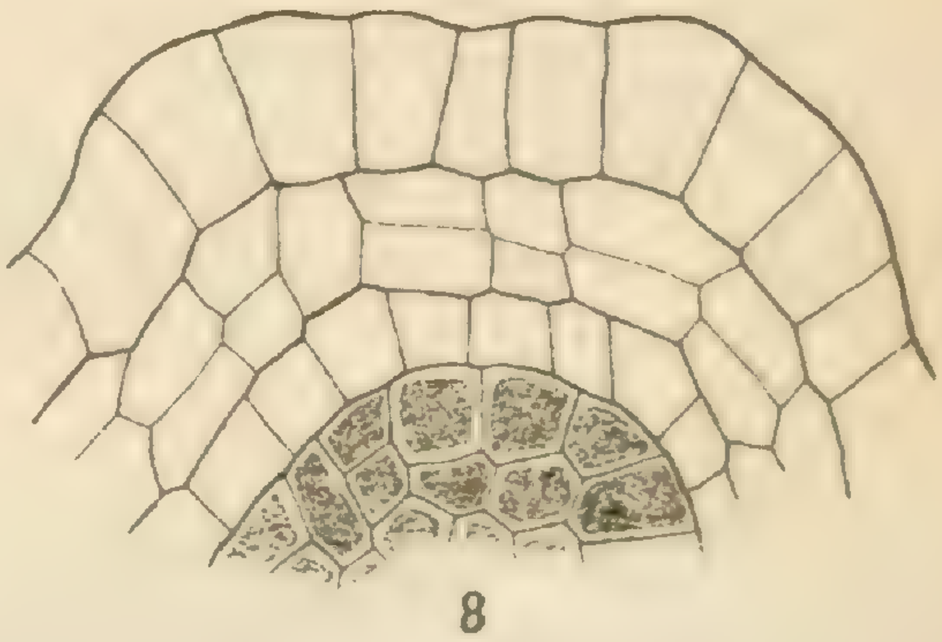

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Of the three sections into which the congress was divided for the special work of the week, perhaps the most important was the "Section on nomenclature." The meetings of this section were held on the Exposition grounds in Festival Hall.

As is well known, the Vienna Congress in 1905 selected LINNAEUS' *Species plantarum* (1753) as the starting point for the nomenclature of the seed plants (Spermatophytes) and vascular cryptogams (Pteridophytes). It also established the general principles and codified the rules which form the *rules of nomenclature for plants*. In dealing with the "cellular cryptogams" certain problems were presented which the Vienna Congress decided should have special consideration, namely the question of different, later starting points for the nomenclature of different groups of the "cellular cryptogams," and the problems connected with the nomenclature of the fungi possessing a pleomorphic life cycle.

As to the starting point for the nomenclature of plants, it is well known that there were two opinions, as follows: (1) that there should be a single date recognized for the beginning of the nomenclature of all plants; this opinion was based on the principle of uniformity in time or date as the starting point; (2) that there might be several different (multiple) dates or starting points for the nomenclature of different groups; this opinion was based on the principle that *uniformity in the selection of the earliest comprehensive work treating a group, large or small, in a somewhat modern sense*, was of more importance than the principle of uniformity of date. Therefore the Vienna Congress wisely decided to refer the consideration of the nomenclature of the "cellular cryptogams" to the Brussels Congress in 1910, in order that these problems might be studied in the meantime.

Since it will be several months before the complete proceedings of the Brussels Congress can be published, we present here, for the benefit of American botanists, a brief statement of the most important legislation enacted by the "Section on nomenclature."

On Tuesday, the section began the consideration of the motions relating to the nomenclature of the "cellular cryptogams," and, with the exception of Thursday, which was devoted wholly to excursions, the work, together with the motions relating to paleobotany and phytogeography, was continued throughout the week. The different groups were taken up in the order in which they were presented in the preliminary publication, including the various motions, the result of the preliminary voting by the special commissions, the comments of the *rapporteur général*, and the provisional draft of rules. In general session of the section it was voted to postpone the consideration of the bacteria, diatoms, and flagellates, and to take

LINNAEUS' *Species plantarum* (1753) as the starting point for the nomenclature of the Myxomycetes.

At the opening of the session after the noon recess it was suggested that an adjournment of the session be taken for an hour in order to allow all the specialists in the different groups of cryptogams who were present to hold an informal conference for the purpose of agreeing upon recommendations as to the dates for the starting points of nomenclature which would be acceptable to them. These recommendations were presented to the section on Tuesday afternoon and Wednesday morning, and were adopted as rules without further discussion, no one expressing a desire to discuss them in general session. The majorities[4] in favor of the different votes were very large, in the case of fungi, for instance, 130 to 4. The dates adopted by the Brussels Congress, therefore, for the starting points for the nomenclature of the "cellular cryptogams" are as follows:

MYXOMYCETES.—LINNAEUS, *Spec. plant.*, 1753.

FUNGI.—FRIES, *Syst. Myc.*, 1821–1832, except for the Uredinales, Ustilaginales, and Gasteromycetes, which date from PERSOON'S *Synopsis*, 1801.

LICHENS.—LINNAEUS, *Spec. plant.*, 1753.

ALGAE.—GOMONT, *Nostocaceae homocysteae*, 1892–1893; BORNET et FLAHAULT, *Nostocaceae heterocysteae*, 1886–1888; RALFS, *British Desmidiaceae*, 1848; HIRN, *Oedogoniaceae*, 1900; LINNEAUS' *Spec. plant.*, 1753, for all other algae except the Chroococcaceae.

BRYOPHYTES.—HEDWIG, *Spec. musc.*, 1801–1830, for the Mosses; LINNAEUS, *Spec. plant.*, 1753, for the Liverworts.

The general position taken by the congress is well shown in the case of bryophytes, in which the fundamental *Species muscorum* of HEDWIG was adopted for mosses; while for liverworts, on which there exists no work corresponding to the *Species muscorum*, it was decided to go back to LINNAEUS.

Action upon the Chroococcaceae, bacteria, diatoms, and flagellates was postponed for future discussion, partly because it was difficult to select satisfactory works as a basis of nomenclature, and partly because those groups have been studied also by zoologists, and it is therefore necessary to take into consideration zoological as well as botanical treatises.

With regard to the nomenclature of the imperfect fungi, the following rule was adopted:

[4] The voting on these questions, and some others, was taken by a count of the number of votes to which each delegate was entitled, and the number of votes cast was therefore greater than the actual number of delegates present. On certain general questions the voting proceeded simply by a show of hands.

FUNGI WITH PLEOMORPHIC LIFE CYCLE.—1. The different successive stages of the fungi with pleomorphic life cycle (*anamorphoses, status*) can bear only a single generic and specific name (*binome*); that is to say, the oldest, from the starting point of the nomenclature of the fungi, which has been applied to the perfect stage, provided that in other respects it conforms to the rules.

2. For the purpose of nomenclature it is agreed that the perfect stage of fungi with pleomorphic life cycle is that which bears the ascus in the Ascomycetes, the basidium in the Basidiomycetes, the teleutospore in the Uredinales, and the spore in the Ustilaginales.

3. Generic or specific names applied to imperfect stages may not be used to replace a name applied to one or more species, any one of which contains the perfect stage.

Citations of pre-Friesian or of pre-Persoonian names follow the rule. Examples: *Boletus edulis* Fries, not *B. edulis* Bull.; *Polyporus ovinus* Fries, not *P. ovinus* (Schaeff.) Fries. Writers who prefer, however, may write *Boletus edulis* Fries ex Bull.; *Polyporus ovinus* Fries ex. Schaeff., etc.

Reverse of See Code

It is recommended in the case of biological species (*formes speciales*) among the rusts that authors who prefer to employ double names take them from the names of the host plants. A recommendation which was offered as applying to the fungi, namely that when a new genus is published, if there are more than one species the author should cite one as the type species, or if only one species, that one to be regarded as the type of the genus, was adopted and made to apply to all plants.

The expression of opinion on the desirability of having extensive lists of *genera conservanda* was so strong that it was practically unanimous, and commissions were appointed to prepare such lists in the fungi, lichens, algae, mosses, and liverworts.

The following action was taken in regard to *genera conservanda* in the Pteridophytes, and additional ones in the Spermatophytes presented for consideration at Brussels. *Selaginella* was placed among the *genera conservanda*, while the remaining genera in the proposed list of Pteridophytes were rejected.

A commission, which had been appointed for the purpose in advance of the congress, carefully considered the additional *genera conservanda* among the Spermatophytes in the list proposed by JANCHEN, and recommended that 21 or 22 names be stricken out. The list as amended, with the addition of the name *Welwitschia*, was adopted.

The motion to amend the Vienna rules by striking out the clause requir-

ing a Latin diagnosis of new genera and species was voted down Monday afternoon, along with several other motions of a general nature. The question was discussed, however, at a later time when considering a motion by the paleobotanists, to the effect that a diagnosis be required only in one of the following languages: French, English, German, or Italian. This discussion broadened into a general one, and although it was defeated the discussion showed that there was a strong sentiment against the Latin requirement, especially on the part of the American botanists, and the subject will probably be brought up again for discussion at the next congress.

With reference to the question of nomenclature in phytogeography, the following principles were adopted, and the commission, considerably enlarged, was continued.

1. Nomenclature is to be avoided, and the expression *terminology* is rather to be employed.

2. When technical words are employed, a clear definition of them should be given in the sense in which the writer uses them, and also where a term is used in a sense different from that in which it has formerly been employed.

3. It is recommended to use terms taken from living (vulgar) languages to designate associations, etc., and reserve expressions of Greek or Latin origin for higher units, where there are rarely equivalents in the living tongues (examples: mesophytic, hydrophytic, etc.).

4. The principle of priority has no legal value in phytogeography. Terminology is very different from nomenclature, and must be subject to change in order to bring it in harmony with the change of ideas in the interpretation of facts.

5. A recommendation for the establishment of clear phytogeographical maps was adopted.

6. Definition of ecology: Phytogeographical ecology is the study of plants and plant associations in their relations with the medium (surrounding medium or environmental conditions).

7. Without giving a definition of the words *formation* and *association*, the section recommends the use of "formation" in a wider ecological sense, and "association" in a more restricted, floristic sense. For example, meadow, prairie, etc., are formations; but an alpine meadow on granitic soil in central Switzerland is an association.

8. It was decided to publish a dictionary of phytogeographic terminology, containing all the pertinent expressions used in phytogeographical and floristic works, with the original definitions and bibliographical references, and their equivalents in English, French, and German.

9. It was proposed that when such words as *zone* and *region* are used in different senses in different countries, to employ new and clear expressions; for example, *étage* (level or floor) = *Höherenregion; Tieferenregion* of the Germans = *zone altière* or *zone abysssale* of the French.

10. A commission was named for the above purpose, consisting of the present members, with many additions, giving the committee power to add still others.

In the publication of the proceedings of the congress, the rules and recommendations adopted at Brussels will be incorporated in their proper places with those adopted at Vienna, the latter being reprinted, so that the rules of nomenclature for plants will be presented in a single and convenient brochure.

The members of the commission on the nomenclature of the cryptogams are greatly indebted to Dr. BRIQUET for summarizing in a comprehensive manner the many different and often conflicting views expressed by the specialists of the commission in their preliminary correspondence. DR. BRIQUET also rendered a most important service in interpreting the remarks made by different speakers in French, English, and German, so that they were understood by all those present. Professor FLAHAULT, Professor MANGIN, and Professor ENGLER, who presided over the different sessions, performed their duties in such a way as to deserve the hearty thanks of all the members, combining a courteous and affable manner with a strictly business management.—W. G. FARLOW and GEO. F. ATKINSON, *Paris, May 28, 1910.*

CURRENT LITERATURE

BOOK REVIEWS

Heredity as an exact science

Problems of evolution have taken a dominant place in biology ever since the appearance of DARWIN'S *Origin of species.* During the latter part of the last century there was little important progress made, though there was an abundance of academic discussion and repeated analysis of data recorded by DARWIN and a few other observers; but already in the closing years of the century a reaction had set in. With the beginning of the present century this reaction reached its first important expression with the appearance of DE VRIES'S *Mutationstheorie*, which marked the beginning of a new epoch in the study of the various factors of evolution, an epoch not inappropriately called the "era of *experimental* evolution." Other branches of biology have exhibited at the same time a corresponding development. Instead of pure speculations, and of generalizations from observations uncontrolled by experimental conditions, there has been a swiftly growing demand for greater exactness in observations and for experimentation.

As an essential part of the reaction, the development of mathematical methods by Professor KARL PEARSON and a few others promised for a time the key to the riddles of evolution. This movement, led by a pure mathematician, developed a series of beautiful methods for the mathematical analysis of data and the comparison of variations. These methods are of the greatest importance when rightly used, but owing to the almost invariable lack of an equally keen *biological* analysis, the applications of these methods have led to a largely spurious product, whose showing of depth and accuracy has been illusive, not because the methods are faulty, but because of their application to data which did not supply the one fundamental assumption of homogeneity upon which the whole biometrical system is based.

Parallel with this movement toward the use of mathematically precise methods, there has been a rapidly increasing utilization of pedigree culture, or genetic methods involved in efforts to distinguish between mutations and fluctuations, and in Mendelian investigations in heredity, which methods lay stress chiefly upon biological analysis. The antagonism of active workers with biometric and genetic methods in the study of heredity scarcely permitted it to be hoped that a work might soon appear which would give a sound and well-balanced treatment of heredity, utilizing the results gained by both biometry and genetics. On the one hand were the mathematical writings of Professor PEARSON and a number of his students, in which mathematical methods are

applied to data without a preliminary biological analysis to determine whether they were indeed homogeneous, as they were assumed to be; on the other hand, the writings of Professor BATESON and many others dealt purely with alternative types so different from each other that they could be classified by ordinary inspection, and ignored entirely the fundamental value, and indeed the necessity, of biometrical methods in the study of less divergent types.

It has remained for Dr. JOHANNSEN[1] of Copenhagen, himself an ardent student of quantitative variation by biometrical methods, harmoniously to combine the mathematical analysis with a biological analysis of his material, that enables him to present a thoroughly well-balanced treatment of heredity and variation in the light of all these recent refinements of method. His book is presented in the form of twenty-five lectures, which give the clearest and simplest discussion of the statistical methods and their exact significance which has yet appeared. His full, elementary, and illuminating explanations of all the biometrical methods, with simple examples showing their usefulness and their limitations, are a noteworthy contribution, since they render an otherwise difficult and to many persons distasteful subject easily intelligible to anyone who will seriously undertake its mastery. While explaining the meaning of all the biometrical methods and their importance in the exact investigation of variation and heredity, the author continually lays stress upon the fact that these methods are instruments whose usefulness depends upon the quality of the data to which they are applied. Much attention is given to irregular, one-sided, or bimodal variation curves, and it is shown that these different types of curves may be produced by any one of several different causes, and that therefore the occurrence of such curves gives no indication of the interpretation which is to be placed upon them. The interpretation must always come by biological analysis.

The biological conception which forms the keynote of the author's entire discussion is *the permanence of the elementary types* which collectively make up all the systematic species of plants and animals. This is essentially the same conception as the "elementary species" of DEVRIES, but by JOHANNSEN it is given an experimental support of such consistency and magnitude as to place it upon a much firmer basis than it has had heretofore. The existence of such permanent types was first given a biometrical demonstration by JOHANNSEN in his *Ueber Erblichkeit in Populationen und in reinen Linien* (1903), and the present work is in large measure an elaboration and application of the conclusions reached in that paper, supported by the results of a number of added generations and additional critical experiments.

The author's keen analysis of the different kinds of types is having a large influence upon present discussions of heredity and evolution. For the elemen-

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[1] JOHANNSEN, W., Elemente der exacten Erblichkeitslehre. Deutschen wesentlich erweiterte Ausgabe in fünfundzwanzig Vorlesungen. pp. vi+516. *figs.* 31. Jena: Gustav Fischer. 1909.

tary forms—whether "elementary species" or "varieties" in the DeVriesian sense—he has proposed the convenient term *biotypes*. He also distinguishes them as *genotypes*, that is, collections of individuals having like germinal characters to distinguish them from mixtures of individuals having like external characters, but of unlike germinal composition. To these latter mixtures, whose uniformity is only apparent, he gives the name *phenotypes*.

Heredity is recognized as only one of many factors involved in evolution, and the author does not even attempt to enumerate the other factors, discussing briefly only such other evolutionary factors as are directly related to the question of permanence of types, for example, natural selection, Weismannism, direct influence of environment, inheritance of acquired characters, etc. He dismisses all which are not based upon a clear distinction between the different kinds of variation and the different kinds of types as purely speculative, and therefore as having no place in the exact science of heredity.

The author recognizes that there may be several ways in which new biotypes come into existence, for example, by changes in the characters of the genes or determiners, loss of genes, combinations of different genes through hybridization, etc., but devotes relatively little attention to this phase of the subject.

While less than 100 pages are given to the results of genetic studies in mutation and hybridization, these subjects are treated in a very satisfactory manner. It is impossible in so short a space nearly to cover these fields in detail, and the method used is the same as in the biometrical part of the book, appropriate examples being introduced to illustrate each phase of the subject, no attempt being made to give a comprehensive account of the many investigations which have been made. With a detailed account of the recent work in Mendelian heredity, we are fortunately supplied at the present time by BATESON'S most recent book[2] on the subject, which, together with this book by JOHANNSEN, gives us a practically complete discussion of what has been done in the study of heredity by exact scientific methods.

While JOHANNSEN'S book is written in German, and is therefore less accessible to the entire English-reading public than might be wished, he has fortunately written with great simplicity and directness, and thus his work is more easily read than is often the case. The author has been criticized by German reviewers because of certain mistakes in German idiom, but the slight departures from the pure German idiom always occur in the direction of the Danish idiom, which is more nearly like the English; consequently, his book is more easily read by English readers than it would be if it followed the German idiom more closely. The value of the work is greatly enhanced by the fact that the author's discussions are illustrated at every point by detailed examples from his own incisive experiments. It is, therefore, a treasure-trove of new knowledge, leading to conclusions which are certain to have a large place in the future

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[2] BATESON, W., Mendel's principles of heredity. pp. xiv+396. *pls. 6. figs. 37.* Cambridge: University Press. 1909.

discussions of heredity and evolution. The book is worthy of a place beside DARWIN'S *Origin of species* and DEVRIES'S *Mutationstheorie*, and is certain to be rated as a classic example of the new spirit which has entered into biological investigation in the beginning of the twentieth century.—GEO. H. SHULL.

Outlines of bacteriology

The scope of a work on bacteriology by ELLIS[3] is outlined in the following sentence of the Introduction: "This book is intended to serve as an introduction to bacteriology in all its branches, though more attention has been bestowed on that aspect of the subject which is of the most interest to students of technical and agricultural bacteriology."

Bearing the above introductory sentence in mind, the reviewer is the more impressed by the apparent "errors of omission and commission," the lack of facile expression, misstatements of fact, and in places the absence of a knowledge that denotes real intimacy with certain phases of the subject to be presented. And it is marvelous that the firm of Longmans, Green & Co., should have undertaken the publication of the volume.

Without touching upon numerous smaller mistakes and errors, attention may be drawn to the prominence given the author's views upon the supposed very general flagellation of the members of the Coccaceae (pp. 19, 20). It might be well to point out that those views are not yet by any means concurred in by many eminent authorities.

The crudity of the method recommended for the observation of the germination of spores (p. 32) is brought into relief when compared with the superior advantages afforded by the use of the hanging-drop, or the hanging agar-block on the warm stage.

In the light of the best American practice, the method advised for the handling of gelatin petri dish cultures is incomparably cumbersome and unnecessary (p. 47); while the strictures passed upon the use of agar under similar conditions are scarcely warrantable (p. 49).

In his discussion of the effect of the electric current upon bacterial life, it would seem that the author had not read far enough afield, else the statements made by Professor J. BEHRENS in LAFAR'S *Handbuch d. techn. Mykologie* (vol. I, sec. 99, p. 455) would have vastly modified his opinion.

Page 61 gives undue prominence to MELTZER'S ideas regarding the adverse action of moderate degrees of continuous vibration upon bacterial cells. It may be said that those views no longer carry weight.

In the chapter on sterilization (p. 85) are to be found the following remarkable statements in reference to the sterilization of the air of a room: "It may at once be stated that no gas is a disinfectant. . . . . Obviously, therefore, if we wish

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[3] ELLIS, DAVID, Outlines of bacteriology (technical and agricultural). 8vo. pp. xii + 262. *figs. 134.* London: Longmans, Green & Co. 1909. *7s. 6d.*

to purify a room, our only chance consists in spraying the walls, the floors, and the objects in the room with a reliable liquid disinfectant. This tends to purify the places from whence the air derives its supply of bacteria." The admirable work of CHICK on the action of disinfectants receives no comment, whereas MIQUEL'S work, so long out of date, is given great prominence.

In the chapter on sewage and sewage disposal (p. 239) are to be found remarks that in this country at least would be deemed erroneous, improper, and inadvisable. For instance, who would willingly subscribe to the following: "There is great similarity between *Bac. typhosus* and *Bac. coli communis*, an organism which is very common in sewage, and which is strongly suspected of being the cause of epidemic diarrhea, though positive proof is still wanting"? Dr. ELLIS condemns the methods of killing off bacteria in sewage by antiseptics as "not practicable," whereas RIDEAL in his own country, and PHELPS and CARPENTER and others in the United States, have shown how valuable an agent is calcium hypochlorite in this direction.

In the section heading "Disposal without purification" (p. 247), discussing the disposal of the contents of cesspools, the author writes: "The other [insoluble] substances that in larger places usually find their way to the sewage drain are thrown broadcast on to any convenient spot, such as a roadside or a neighboring common. This method is efficient enough for very small places, though it must detract somewhat from the healthiness of village life." It is to be regretted that Dr. ELLIS puts himself on record as condoning such a practice; no matter under what conditions of life, the practice is sufficiently vile and unsanitary to be most strongly condemned.

It is very noticeable that no chapter on the biological methods of water purification found a place in the book, despite its importance to technical students.

One cannot turn over the pages of the book without remarking upon the inexcusable crudeness of some of the drawings, which actually mar what otherwise makes a most presentable volume.—NORMAN MACL. HARRIS.

Vegetable proteins

Another of the monographs on biochemistry edited by PLIMMER and HOPKINS has just appeared,[4] and deals with vegetable proteins. It is hardly necessary to state to biological chemists or plant physiologists that no one can speak more authoritatively upon this topic than OSBORNE. Plant physiologists, of whom a fundamental knowledge in several accessory sciences is demanded, are sure to welcome a work of this kind. It shows directness and force that comes from the author, who is the greatest producer in the subject he is discussing. The bibliography consists of 608 citations.

A list of the chapter headings will give a good idea of the scope of the work: historical review; occurrence of proteins in different parts of plants and their

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[4] OSBORNE, THOMAS B., The vegetable proteins. 8vo. pp. xiii + 125. New York: Longmans, Green & Co. 1909.

general characteristics; isolation and preparation of seed proteins; basic and acid properties of proteins; solubility of vegetable proteins; precipitation of vegetable proteins; denaturing of vegetable proteins; physical constants of vegetable proteins; products of hydrolysis of vegetable proteins; classification of vegetable proteins; some physiological relations of vegetable proteins to the animal organsim and the biological relations of seed proteins to one another.

The plant physiologist will welcome this work expecially, for most discussions of proteins deal in the main with animal proteins.—WILLIAM CROCKER.

MINOR NOTICES

A new catalogue of Connecticut plants.—The Connecticut Botanical Society, through a committee of six of its members, has issued recently a *Catalogue of the flowering plants and ferns of Connecticut*.[5] The publication has been modestly termed a *catalogue*, but it is far more than a mere list of plants of the state. The scientific and common names of the plant are given, as well as limited synonomy, habitat, distribution, and citation of exsiccatae; and often a note on the economic import of the species is added.

In the sequence of families and in nomenclature the work accords with the seventh edition of GRAY'S *Manual*. A statistical summary gives the following composition of the flora: number of families 134, genera 621, species 1942, varieties and forms 286; a total of 2228 recognizably distinct plants; and approximately four-fifths of these are indigenous to the state.

The work is an important one to the taxonomic student; and the collaborators have done a commendable service to their state in recording, in available and useful form and with a high degree of accuracy and completeness, their intimate knowledge of the Connecticut flora.—J. M. GREENMAN.

North American Flora.[6]—Volume XXV, part II, is devoted to the Geraniales, as follows: Tropaeolaceae by G. V. NASH, Balsaminaceae and Limnanthaceae by P. A. RYDBERG, Koeberliniaceae by J. H. BARNHART, Zygophyllaceae by A. M. VAIL and P. A. RYDBERG, and the Malpighiaceae by J. K. SMALL. Four new genera of the Malpighiaceae are proposed, namely, *Adenoporces*, *Callaeum*, *Rosanthus*, and *Banisteriopsis*. Several new species are described; these are distributed among the following genera: *Impatiens* (3), *Fagonia* (3), *Guaiacum* (3), *Kallstroemia* (6), *Mascagnia* (2), *Hiraea* (1), *Triopteris* (1), *Tetrapteris* (2), *Banisteriopsis* (2), *Banisteria* (2), *Stigmaphyllon* (1), *Thryallis* (1), and *Malpighia* (5).—J. M. GREENMAN.

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[5] GRAVES, C. B., FAMES, E. H., BISSELL, C. H., ANDREWS, L., HARGER, E. B., and WEATHERBY, C. A., Committee of the Connecticut Botanical Society. Catalogue of the flowering plants and ferns of Connecticut growing without cultivation. Bulletin No. 14, State Geological and Natural History Survey. 8vo. pp. 569. Hartford, Conn. 1910.

[6] North American Flora, vol. XXV, part II, pp. 89–171. New York Botanical Garden. 1910.

NOTES FOR STUDENTS

Current taxonomic literature.—L. ABRAMS (Bull. Torr. Bot. Club **37**:149–153. 1910) has described 4 new species of flowering plants from California.—O. AMES (Phil. Journ. Sci. Bot. **4**:663–676. 1909) in continuation of his studies on Philippine orchids records 30 species, 11 of which are new to science.—S. F. BLAKE (Fern Bull. **18**:9, 10. 1910) records a new variety of *Lycopodium tristachyum* Pursh from New Hampshire.—I. BOLDINGH (Recueil Trav. Bot. Néerl. **6**:1–36. 1909) under the title "A contribution to the knowledge of the flora of Anguilla (B.W.I.)" lists about 150 species of flowering plants. The list is based on collections made on the island by Mr. BOLDINGH in September of 1906.—F. BØRGESEN (Bot. Tidssk. **30**:1–19. *pls. 1, 2.* 1910) has published the results of his studies in the Florideae collected in the waters of the Danish West Indies, describing and illustrating 5 new species.—M. BURRET (Bot. Jahrb. **44**:198–238. 1910) presents the results of an extended taxonomic study of the genus *Grewia*, accompanying the same by a key to the African species.—B. CHABAUD (Rev. Hort. Paris **82**:58–60. *fig. 18.* 1910) has published a new species of palm (*Sabal uresana*) indigenous in the state of Sonora, Mexico.—H. CHRIST (Rep. Nov. Sp. **8**:17–20. 1910) has published 7 new species of ferns from Costa Rica.—A. COGNIAUX, A. LINGELSHEIM, F. PAX, and H. WINKLER (*ibid.* 1–6) under the title "Plantae novae bolivianae IV" have published 11 new species and 2 new varieties of Bolivian flowering plants.—A. ENGLER (Bot. Jahrb. **44**:137–155. 1910) has published 31 new species of the Burseraceae from Africa; the same author (*ibid.* Beibl. 101, p. 34) proposes a new genus (*Scirpodendron*) of the Cyperaceae from Africa.—E. GILG (*ibid.* 15–19) describes and illustrates a new species of *Marckea* (*M. Peckoltiorum*) from Brazil.—W. FAWCETT and A. B. RENDLE (Journ. Bot. **48**:106–108. 1910) in continuation of their studies on the orchids of Jamaica have published 4 new species.—E. L. GREENE (Leafl. Bot. Obs. and Crit. **2**:25–88. 1910) has characterized about 90 new species of flowering plants mostly from western United States.—E. HASSLER (Bull. Soc. Bot. Genève II. **2**:32–36. 1910) has characterized 3 varieties and 6 forms of *Indigofera campestris* Bong. from Paraguay. The same author (Rep. Nov. Sp. **8**:28–31, 34–47, 66–73, 113–132, 204–210. 1910), in cooperation with different specialists, has published several new species and varieties of flowering plants from South America. Two new genera of the Malvaceae are proposed, namely *Blanchetiastrum* from Brazil, and *Bastardiopsis* from Brazil and Paraguay.—A. VON HAYEK (Oesterr. Bot. Zeitschr. **60**:89–93. 1910) has characterized a new genus (*Degenia*) of the Cruciferae, based on *Lesquerella velebitica* Degen.—A. A. HELLER (Muhlenbergia **6**:13–32. 1910) records the results of further studies on the "Nevada lupines" and includes descriptions of 4 new species.—R. H. HOWE, Jr. (Bull. Torr. Bot. Club **37**:1–18. *pls. 1–7.* 1910) gives a revision of the genus *Usnea*, as represented in North America north of the 15th parallel, recognizing 4 species.—E. KOEHNE (Rep. Nov. Sp. **8**:16, 17, 165–167, 196–199. 1910) has published 6 new species and 4 new varieties of *Cuphea* from the Lesser Antilles and Paraguay.—F.

KRÄNZLIN (*ibid.* 97, 98) has described 2 new species of orchids from the Philippine Islands.—G. KÜKENTHAL (*ibid.* 7, 8) under the heading "Cyperaceae novae I" describes new species and varieties in the genus *Carex*, some of which are from America.—K. KRAUSE (Bot. Jahrb. **44**: Beibl. 101, pp. 9–14. 1910) has published several new species of Araceae from South America and the Philippine Islands.—TH. LOESENER (*ibid.* **44**:156–197) gives a synoptical revision of the genus *Salacia*, recognizing 64 species, of which 25 are new to science.—W. MOESER (*ibid.* 239–345) characterizes the different natural groups of species in the genus *Helichrysum*, accompanying the same by determinative keys, and adding about 30 species and several varieties new to science.—R. PILGER (*ibid.* Beibl. 101, p. 7) has published a new species of *Valeriana* from southern Brazil.—J. W. PALIBINE (Bull. Soc. Bot. Genève II. **2**:17–21. 1910) presents an article on the subsection BAICALIA of the genus *Oxytropis*, describing one new species and transferring *Arogallus Bellii* Greene to *Oxytropis*.—F. PAX (Rep. Nov. Sp. **8**:161, 162. 1910) has published 4 new species of Euphorbiaceae from Brazil and Mexico.—H. E. PETERSEN (Bot. Tidssk. **29**:345–429. 1909) under the title "Studier over Ferskvands-Phykomyceter" describes several new species and proposes one new genus (*Pythiomorpha*) from Denmark.—A. PULLE (Recueil Trav. Bot. Néerl. **6**:251–293. 1909) in continuation of his studies on the flora of Surinam publishes a second article including 18 new species of flowering plants.—C. B. ROBINSON (Phil. Journ. Sci. Bot. **4**:687–698. 1909) gives a synoptical treatment of the Philippine Boraginaceae, recognizing 10 genera to which are referred 21 species.—P. A. RYDBERG (Bull. Torr. Bot. Club **37**:127–148. 1910) under "Studies on the Rocky Mountain flora XXI" describes 27 new species and makes several new combinations in the Compositae.—F. J. SEAVER (Mycologia **2**:48–92. *pls. 20, 21.* 1910) continues his monographic treatment of the Hypocreales of North America, publishes several new species, and proposes two new genera (*Chromocrea* and *Chromocreopsis*).—H. and P. SYDOW (Ann. Mycol. **8**:36–41. 1910) have published 22 new species of fungi from the Philippine Islands.—W. TRANZSCHEL (*ibid.* 1–35) in an article entitled "Die auf der Gattung Euphorbia auftretenden autöcischen Uromyces-Arten" has published several new species of fungi parasitic on different American euphorbias.—P. WILSON (Bull. Torr. Bot. Club **37**:85, 86. 1910) describes a new species of *Amyris* from Mexico and publishes several new combinations in the genus *Zanthoxylum*.—E. O. WOOTON (*ibid.* 31–41) in an article entitled "The larkspurs of New Mexico" recognizes 12 species for the state, 5 of which are described as new; a key to the species accompanies the descriptive matter.—Different authors (Kew Bull. 55–60. 1910) under the title "Diagnoses Africanae XXXIV" have published several new species and described a new genus (*Megabaria*) of the Euphorbiaceae.—J. M. GREENMAN.

Respiration.—KUIJPER[7] has studied the effect of various temperatures on the amount of CO_2 produced by the seedlings of *Lupinus luteus*, *Pisum sativum*,

[7] KUIJPER, J., Ueber den Einfluss der Temperatur auf die Atmung der höheren Pflanzen. Extrait Rec. Trav. Bot. Néerland. **7**: pp. 109. *pls. 3.* 1910.

and *Triticum vulgare*, with the view of testing the applicability of the ideas set forth in BLACKMAN'S[8] "optima and limiting factors" to the process of respiration. In general the experiments were run six hours, and the CO_2 production determined for each hour. Up to 10° the CO_2 produced per hour was constant for the six hours. At higher temperatures, up to 20°, there was a rise for four or five hours. This rise is hard to explain in the light of the facts that the seeds were germinated at approximately 20°, that it occurred regardless of the age of the seedlings, and that it was followed by a corresponding fall. At constant temperatures above this, up to 40°, a fluctuation in CO_2 production was apparent. Especially between 30° and 40° this manifested itself by a rapid fall for the first two hours, followed by a later rise ranging over one to two hours, followed by a later continuous fall. The author assumes that two distinct processes are differently affected by the continuous high temperature: one early depressed, marking the fall; the other later stimulated, showing the rise. This fact he suggests may be related to the double nature of CO_2 production in respiration noted by PALLADIN, in which he assumes the action of oxidase on the one hand and of carbonase on the other. At still higher temperatures there is a continual fall in CO_2 production. The temperature at which one type of behavior changes to another is determined by the nature of the stored food, as the following tables show:

	Lupinus	Pisum	Triticum
Rise noticeable	15–20°	20–25°	30°
Fluctuation	20–25°	30°	35°
Continual falling	25°	35°	40°
Protein	37%	22%	12%
Starch	none	54%	74%

The VAN'T HOFF law applies for *Pisum* and *Triticum* from 0°–20°, and for *Lupinus* up to 25°. The coefficient for a temperature difference of 10° lies between 2 and 3. The continual falling in CO_2 production with continual exposures at higher temperatures agrees with BLACKMAN'S results. BLACKMAN found that in photosynthesis the initial rate at any given high temperature (30–40°) could be figured in two ways, giving agreeing results: by applying the VAN'T HOFF coefficient to the measurements at lower temperatures where the rate is constant, or by taking several later determinations at the given temperatures and from these extrapolating the initial value. KUIJPER finds that these methods will not apply to the CO_2 yield in respiration, because of the appearance of the two antagonistic factors at temperatures between 30° and 40°, and because of the non-application of the VAN'T HOFF law at the higher temperatures.—WILLIAM CROCKER.

Permeability.—CZAPEK[9] has published a preliminary article upon the effect of various reagents upon the precipitation of tannins in plant cells by means of caffein and ammonium carbonate. If slices from the epidermis of *Echeveria*

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[8] BLACKMAN, F. F., Annals of Botany **19**:281–295. 1905.

[9] CZAPEK, F., Versuchs über Exosmose aus Pflanzenzellen. **Ber. Deutsch. Bot. Gesell. 28**:159–169. 1910.

leaves are placed in $n/1000$ acid for 24 hours, and then treated with caffein solution, no tannin is precipitated; while the controls kept in water show a heavy precipitate. The acid solution showed a strong tannin test with iron salts. CZAPEK concludes that the acid renders the *Plasmahaut* permeable to tannins, and that they gradually diffuse out. In strong acids he finds $n/6400$ the critical (minimum) concentration for inducing marked permeability. This is the concentration at which KAHLENBERG and TRUE found growth to cease. CZAPEK believes the stoppage of growth is directly due to reduced turgor, resulting from the induced permeability of the protoplasm to contained substances. He recognizes that injuries appear in concentrations below the critical concentration for permeability. Various other substances give similar results. The critical concentration for phenol is 0.58 per cent or $n/16$; for resorcin, di-hydric phenol, 2.85 per cent or $n/4$; for pyrogallol tri-hydric phenol $n/4$. Among alcohols, the critical concentrations were methyl 15 per cent, ethyl 10–11 per cent, normal and iso-propyl 4–5 per cent, iso-butyl 1–2 per cent, amyl 0.5 per cent. In acetic acid the critical concentration is below that determined by its acid properties. The effect of external conditions upon the permeability of protoplasmic and other plant membranes is a subject that deserves much attention from plant physiologists. Animal physiologists are teaching us much in this field.—WILLIAM CROCKER.

Morphology of Sciadopitys.—LAWSON[10] has published an account of the gametophytes and embryo of *Sciadopitys*, one of the peculiar conifers of eastern Asia. The microspores are binucleate at shedding, and are received upon the so-called pollen cushion, which is the tip of the nucellus differentiated into a loose tissue of large thin-walled cells. During the first season only one more division occurs, that of the generative cell into the body cell and a free stalk nucleus. In the next season the body cell passes toward the tip of the pollen tube, which has entered an archegonial chamber, and there produces two unequal male nuclei. The formation of the megaspore tetrad is peculiar. The division of the mother cell nucleus is not accompanied by wall formation; but the subsequent division of the two daughter nuclei is; so that the tetrad comprises three cells, the middle one of which is binucleate. In these divisions the chromosome numbers prove to be 8 and 16. The innermost megaspore is the functioning one, enlarging very much, and becoming invested by the usual zone of nutritive cells. The female gametophyte is developed as in the majority of conifers, and there are four or six archegonia, each with its own investment of jacket cells and a deep archegonial chamber. A ventral nucleus is formed, but no ventral canal cell. In the development of the embryo, the free nuclei pass to the base of the egg at the four-nucleate stage, and the proembryo finally consists of three tiers of cells and one tier of free nuclei toward the egg cytoplasm. The middle tier of cells becomes the suspensor, while the embryo-forming tier becomes a mass of at least sixteen cells.—J. M. C.

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[10] LAWSON, A. ANSTRUTHER, The gametophytes and embryo of *Sciadopitys verticillata*. Annals of Botany **24**:403–421. *pls. 29–31*. 1910.

The structure of Podocarpus spinulosa.—BROOKS and STILES[11] find the structure of the stem and leaf of *Podocarpus spinulosa* similar to species studied by PENHALLOW and WORSDELL. The wall of the microsporangium is described as similar to that of *Saxegothaea* and *Araucaria* except that the dehiscence is oblique. The male gametophyte agrees with *P. ferruginea* and *P. dacrydioides*, described by JEFFREY and CHRYSLER, having a prothallial complex of eight cells, and occasionally the appearance as of a second derivative of the generative cell. The course of the vascular bundles in the ovulate sporophyll is studied in detail and compared with other forms.

That *Podocarpus* is a specialized offshoot from *Saxegothaea*-like ancestors is confirmed by the presence of less mesarch wood than in *Saxegothaea*, the loss of function of some of the resin canals, and the specialized ovulate structure with reduction in size and number of scales. The independence of the vascular supply of the ovule from that of the scale is explained by the greater importance of the ovule in *Podocarpus*. The authors regard Podocarpineae as a natural group, with no very definite connection with Taxineae, no evident relation to Abietineae, but with a probable connection with Araucarineae.—MARY S. YOUNG.

Evolution of plants.—In his presidential address of 1910 before the Linnean Society of London, PROFESSOR SCOTT selected as his subject "Some modern ideas on the course of evolution of plants." It is an outline of the present status of opinion in reference to the evolution of vascular plants, especially as developed by the recent rapid increase of knowledge of paleobotanical material, and is in part a confession of faith. The author evidently believes in the homologous origin of the alternation of generations, and regards the sporophyte of the pteridophyte as developed directly from the thallophyte body. Special attention is given to the views of LIGNIER in connection with this thalloid origin of the cormophyte. The classification of vascular plants proposed in the new edition of his *Studies in fossil botany* is outlined, and the gymnosperm relationships are discussed; while Bennettitales-like forms are still put forward as representing a possible origin of the angiosperms. Perhaps the main thesis of the address is to illustrate among plants the theory of GASKELL, developed in a discussion of the origin of vertebrates, that "each successive group has arisen from some member of the highest group existing at the time."—J. M. C.

Evolution of Pinus.—BAILEY[12] has presented the anatomical characters that seem to be of service in tracing the lines of descent of pines. The cretaceous pines and *Prepinus* are characterized by thick-walled ray parenchyma, "piciform" lateral ray pits, absence of marginal ray tracheids, and abundant

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[11] BROOKS, M. A., and STILES, W., The structure of *Podocarp spinulosa*. Annals of Botany **24**:305–318. *pl. 21*. 1910.

[12] BAILEY, IRVING W., Anatomical characters in the evolution of *Pinus*. Amer. Nat. **44**:284–293. 1910.

tangential pitting of autumnal tracheids. The change in the living pines is seen in the disappearance of thick-walled ray cells, the presence of large compound ray pits, the development of ray tracheids, and the loss of tangential pitting of autumnal tracheids. The type of hard pines represented by *P. resinosa* in North America and *P. silvestris* in Europe is "the most highly developed and specialized condition among living pines." The nut pines (of North America and Asia) have piciform lateral ray pits and thick-walled ray cells, and in these features they are the living pines that approach most nearly to the cretaceous pines. The hard pines of the United States, with the exception of *P. resinosa*, show a great range of variation from piciform to compound lateral ray pits; and the soft pines present a parallel series of gradations.—J. M. C.

Non-available water.—BOVIE[13] has tested the effect of salts upon the non-available water in a soil of crushed quartz. Aside from a full nutrient solution of 0.2 per cent, various amounts of NaCl, ranging from 0.05 to 0.6 per cent, were added. To 100 grams of soil 20 grams of solutions were added. After the plants had grown considerably and the soil moisture was nearly exhausted, the cultures were placed in a special drying chamber of relative humidity of 0.1. Soil was tested for contained moisture when the foliage began to wilt, and when it showed drying. The remaining water was essentially the same regardless of the amount of salt present. Assuming that none of the salts are absorbed by the plants, BOVIE finds that the soil water, at the close of the experiments, in some cases would contain more than 300 per cent of salts, and that much of it must be in the solid form in spite of greatly increased solubility in the thin water films. He also offers some evidence for the movement of water in soils of low water content in the form of vapor, a thing already emphasized by various workers.—WILLIAM CROCKER.

Transpiration stream.—ZIJLSTRA[14] finds that lowering the temperature of sections (20 cm. in length) of stem of intact plants to 0° C. for several days, even under the most favorable conditions for transpiration, does not lead to wilting of the foliage. It is assumed that this renders the living cells of the zone comparatively inactive, without injuring them and without producing injurious or blocking material. The results are contrary to those obtained by the same method by URSPRUNG, who used the results as an argument for the necessity of the activity of living cells to the continuity of the transpiration stream. ZIJLSTRA also conducted a number of experiments on the movement of 0.1 per cent *Säureviolett* (GRÜBLER) in living and dead stems. He also

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[13] BOVIE, WILLIAM T., The effects of adding salts to the soil on the amount of non-available water. Bull. Torr. Bot. Club **37**:273–292. 1910.

[14] ZIJLSTRA, K., Contributions to the knowledge of the movement of water in plants. Reprint from Koninklijke Akad. Wetenschappen te Amsterdam. 1910:574–584.

studied the behavior of plants in which lateral movement of water was made necessary by the ordinary method of incisions on opposite sides. Only the first set of experiments throws any new light on the question of the rise of sap.—WILLIAM CROCKER.

Phylogeny of Filicales.—BOWER[15] has begun the publication of a series of studies in the phylogeny of the Filicales, and the first paper presents the singular and poorly known genus *Plagiogyria*. It is grouped among the Polypodiaceae, and even merged with *Lomaria*, but the position is anomalous on account of the oblique annulus. Several species were secured, both oriental and occidental, and the results may be considered fairly representative for a genus of eleven species. The conclusions are that the genus is quite a distinct one, deserving to stand apart from *Lomaria* or any other genus; that it is relatively primitive, as shown by stelar structure, leaf traces, venation, etc.; that it has resemblances to the Simplices, but that its characters indicate that it is rightly placed among the Pterideae; and that its "mixed" sorus, without any "gradate" sequence of sporangia, combined with its primitive characters and its affinity to the Pterideae, shows that the Mixtae have probably come directly from the Simplices, rather than by any of the Gradatae.—J. M. C.

Geotropism and split stems.—SCHTSCHERBACK,[16] working in PFEFFER'S laboratory, has carried on a series of experiments on the geotropic reactions of split stems. In the main, *Lupinus albus* was used, for in this form the tissue strains between cortex and pith are slight. Splitting cuts the rate of growth even in the vertical position, but two equal halves grow with equal speed in that position. If the two halves are placed horizontally, with the split faces together and horizontal, the lower half is favored in its growth and the upper half greatly inhibited, or even entirely stopped in most cases. Restoring the two halves to their normal vertical position restores them to equal growth, and rotating them 180° on the horizontal axis, to give an interchange of position, gives an interchange of rates of growth. The same geotropic inhibition and favoring of growth occurs in the two separated halves of the stem as occur in their intact condition.—WILLIAM CROCKER.

Relation of living cells to the rise of sap.—RORHARDT,[17] in his voluminous article on the part played by living cells in the rise of sap, has followed the method of wearying the reader with the publication of his notebook, instead of preparing a concise statement of his methods and results. Of the 125 different species of herbs and shrubs native to Germany, representing various monocotyl and dicotyl

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[15] BOWER, F. O., Studies in the phylogeny of the Filicales. I. *Plagiogyria*. Annals of Botany **24**:423–450. *pls. 32, 33. figs. 5.* 1910.

[16] SCHTSCHERBACK, JOHANN, Die geotropische Reaktion in gespaltenen Stengeln. Beih. Bot. Centralbl. **25**[1]:358–386. 1910.

[17] RORHARDT, P. A., Ueber die Beteiligung lebender Zellen am Saftsteigen bei Pflanzen von niedrigen Wuchs. Beih. Bot. Centralbl. **25**[1]:243–357. *figs. 2.* 1910.

families that he has investigated, he finds that the killing of a short zone of a stem or of a petiole results very soon in cutting down the water transport to the parts above, and leads to wilting—the longer the killed zone, the quicker the wilting. He claims that there is no blocking or interfering with the water path, but that the reduced water movement is due to the lack of living cells in the zone killed. This indicates that the continuous rise of sap in small plants, as has been shown to be the case in tall trees, is dependent upon the action of living cells.—WILLIAM CROCKER.

Seedling structure of Gnetales.—HILL and DEFRAINE[18] conclude their account of the seedling structure of gymnosperms by a presentation of Gnetales. A short cotyledonary tube is formed in every case; the cotyledonary traces are two in *Ephedra*, four (in two pairs) in *Welwitschia*, and four or five in *Gnetum;* and all the traces are collateral endarch. The so-called foot in *Welwitschia* and *Gnetum* is described as a parenchymatous growth at the base of the hypocotyl, in the former genus being spadelike and with no vascular supply, and in the latter genus being rodlike and with numerous well-differentiated bundles. The transition to root structure occurs in the lower region of the hypocotyl, in *Welwitschia* and *Gnetum*, immediately below the foot; and in all cases the primary root is diarch.—J. M. C.

"Apogamy" in Pteris.—Miss STEPHENS and Miss SYKES have examined prothallia of *Pteris droogmantiana* furnished by BOODLE. In a brief note[19] they announce that binucleate cells are common; that there has been no nuclear migration, as no surrounding cell is without its nucleus; that the two nuclei arise from the division of the nucleus of an ordinary cell without wall-formation; that the two nuclei thus produced remain separate for some time and then fuse. Just what this performance means is not evident, but perhaps the fuller paper will tell. The note is called one on "apogamy," and presumably there is reason for knowing that these are apogamous prothallia.—J. M. C.

Morphology of Psilotum.—STILES[20] has investigated the anatomical structure of the serial shoots of *Psilotum flaccidum*, one of the two species usually regarded as constituting the genus. Aside from certain anatomical details that distinguish this species from the other (*P. triquetrum*), the main results are that secondary thickening is found in this species also; that mesarch structure occurs in the lower part of the aerial stems; that the sporangiophore trace terminates in the central tissue between the three "confluent" sporangia, as had been shown for *Tmesipteris;* and that no evidence was obtained to decide whether the sporangiophore is "foliar" or is "an organ *sui generis*."—J. M. C.

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[18] HILL, T. G., and DEFRAINE, E., On the seedling structure of gymnosperms. IV. Gnetales. Annals of Botany **24**:319–333. *pls. 22, 23.* 1910.

[19] STEPHENS, E. L., and SYKES, M. G., Preliminary note on apogamy in *Pteris droogmantiana.* Annals of Botany **24**:487. 1910.

[20] STILES, W., The structure of the aerial shoots of *Psilotum flaccidum* Wall. Annals of Botany **24**:373–397. *pl. 25.* 1910.

Removal of cotyledons.—JACOBI[21] has studied the effect of the removal of various amounts of cotyledonary tissue upon the rate of growth of seedlings. In both light and darkness, removal of one cotyledon and even a part of the second early but temporarily stimulates the rate of longitudinal growth of the stem of *Phaseolus multiflorus*. In *Cucurbita Pepo* and conifer seedlings, elongation of the stem is stimulated in darkness, while in light the expanse of the cotyledon is most increased. In *Cucurbita* and the pines, the cotyledons of course bear little food material and function as leaves. The paper adds little that is new.—WILLIAM CROCKER.

Morphology of Cunninghamia.—In 1908 MIYAKE published a preliminary account of the gametophytes and embryo of the monotypic *Cunninghamia*, which was reviewed in this journal (**46**:156. 1908). Now the full paper has appeared,[22] with its excellent plates and photomicrographs. The review referred to includes a synopsis of the most important results, so that it is only necessary to announce the appearance of the full paper.—J. M. C.

Insect galls.—BEUTENMULLER[23] has published two more valuable papers on the American gall-producing insects and their galls. In these two papers he takes up 44 species, including three new ones, gives complete synonomy and bibliography for each, and clear, comprehensive descriptions of both the galls and the insects. This series of papers is of very great value to both the botanist and the entomologist.—MEL T. COOK.

A new disease of apples.—LEWIS[24] has recently described a new species of *Endomyces* (*E. mali*), which he finds capable of producing a slow decay of ripe apples. This is the first species of this family to be reported from the United States, and hence many will be interested in the facts he gives regarding the morphology, spore production, relationship, and cultural behavior of this new species. —E. MEAD WILCOX.

Polarity.—Miss FREUND[25] has made a study of polarity in the twigs of plants. The paper offers nothing new on the subject. Her work might have been far more conclusive if she had been acquainted with the work of MACALLUM,[26] and had applied the cultural methods used by him.—WILLIAM CROCKER.

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[21] JACOBI, HELENE, Ueber den Einfluss der Verletzung von Kotyledonen auf das Wachstum von Keimungen. Flora **101**:279–289. *figs. 2.* 1910.

[22] MIYAKE, K., The development of the gametophytes and embryogeny in *Cunninghamia sinensis*. Beih. Bot. Centralbl. **27**:1–25. *pls. 1–5.* 1910.

[23] BEUTENMULLER, WM., The North American species of *Neuroterus* and their galls. Amer. Mus. Nat. Hist. **28**:117–136. *pls. 8–13.* 1910; and the North American species of *Aylax* and their galls. *Idem* **28**:137–144. *pl. 14.* 1910.

[24] LEWIS, C. E., An *Endomyces* from apple. Bull. Maine Exp. Sta. **178**:45–64. *figs. 58–71.* 1910.

[25] FREUND, VELLA, Untersuchungen über Polarität bei Pflanzen. Flora **1**:279–308. 1900.

[26] MACALLUM, W. B., Regeneration in plants. BOT. GAZETTE **40**:97–120, 241–263. 1905.

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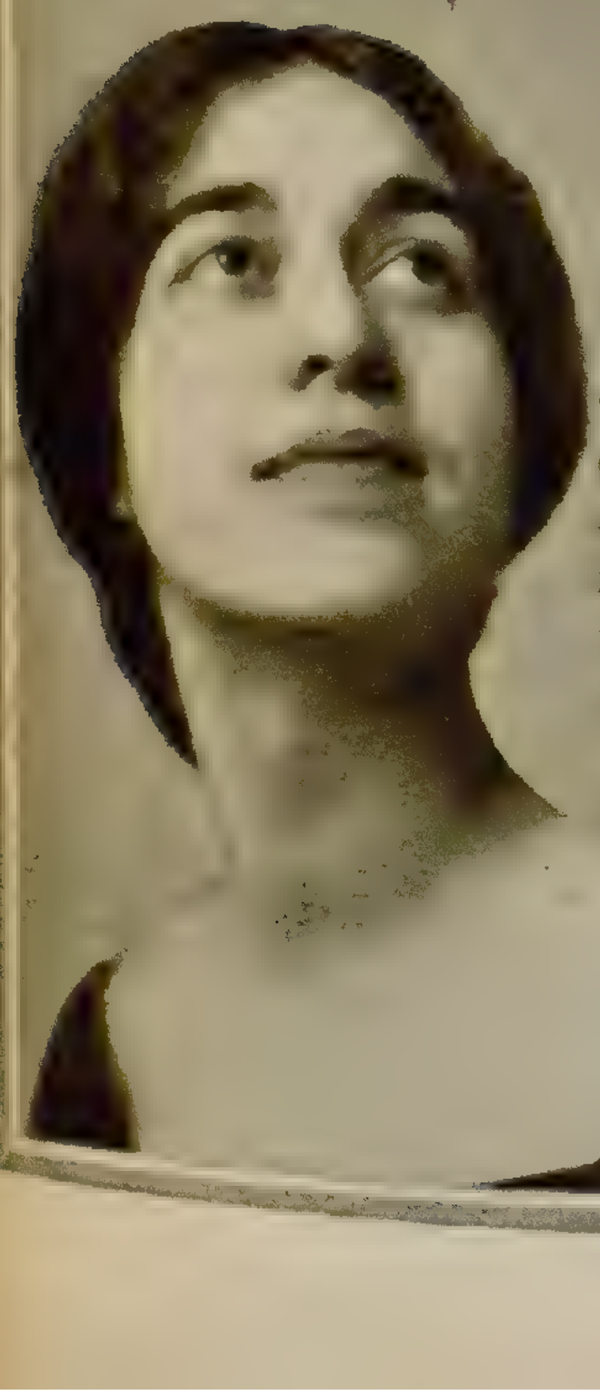

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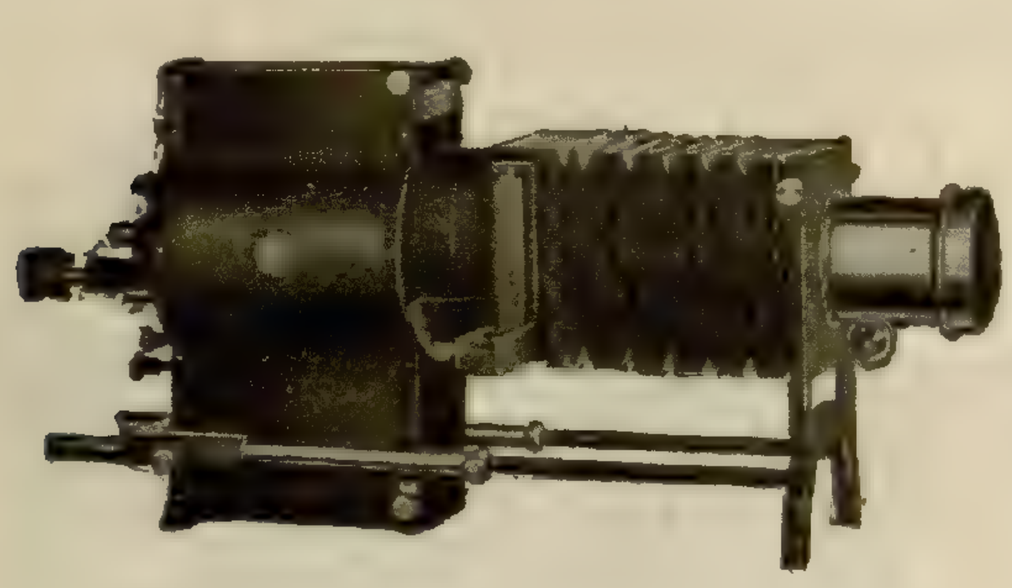

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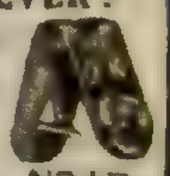

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THE BOTANICAL GAZETTE

October 1910

Editor: JOHN M. COULTER

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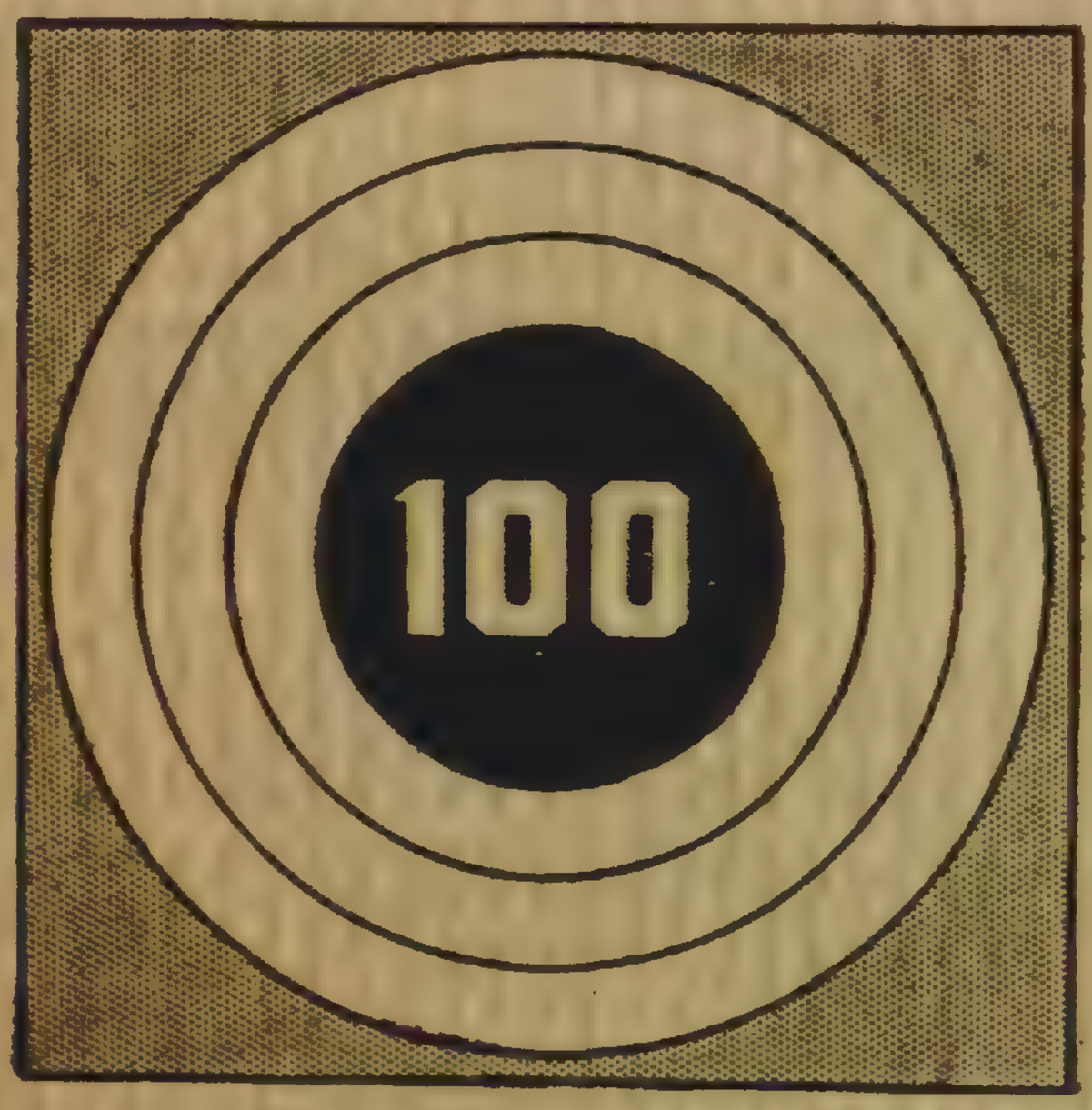

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BOTANICAL GAZETTE

OCTOBER 1910

RELATION OF SOIL MOISTURE TO DESERT VEGETATION[1]

BURTON EDWARD LIVINGSTON

(WITH FOUR FIGURES)

INTRODUCTION.—Of a number of lines of study now in progress, looking toward some quantitative knowledge of the relation obtaining between vegetation and environmental conditions, the determination of the march of soil moisture at Tucson has now progressed sufficiently far to warrant publication. The present paper deals with a continuation of the data upon soil moisture published by the writer under the title: "The soils of the Desert Laboratory domain" in SPALDING'S recent monograph on desert ecology (1). The data there presented comprise observations on soil moisture content extending over the period from October 1907 to April 1908. The period of observation has now been extended to March 1909, thus including both the spring dry season and that of the summer rains. To make the present presentation complete, the observations already published are here included.

RELATION OF SOIL MOISTURE TO OTHER FACTORS.—Just as the evaporating power of the air and the nature of the transpiring organs practically determine the water requirement of plants, so do the soil moisture content and the nature of the root system determine the water supply. Aside from those cases (of toxic soils and soils of high osmotic pressure) where the nature and amount of the solutes in the soil solution exert an influence upon the character of the root system or upon the rate of water absorption

[1] Publication from the Botanical Laboratory of the Johns Hopkins University, No. 16.

by these organs, and aside from those cases where the chemical content of the atmosphere or the character or intensity of illumination exert an influence upon the structure of the transpiring organs or upon the general tone of the plant, the simple relation between soil moisture and the evaporating power of the air appears to be of prime importance in determining the character of the natural vegetation. Over an area such as that here considered, where the air and light conditions are approximately uniform, and where the chemical content of the soil appears not to vary sufficiently to produce variations in plant growth, the possible rate of water supply to plant roots may be supposed to become the limiting condition. This rate of supply depends primarily upon the absolute amount of soil moisture and upon the water-conducting power of the soil.

Soil moisture, of course, depends upon the rate of influx and the rate of removal of water from the soil. The former is determined by the ability of the soil to raise water from the subterranean water table, where such exists, by the amount and time of precipitation or other water entering the soil from above or laterally, and by the water-retaining power of the soil. Water removal from the soil is a resultant of evaporation at the soil surface, downward movement into lower layers, and plant absorption.

Throughout the area here studied precipitation is approximately uniform. Surface drainage, nearly uniform within the extent of each soil type, is quite different (because of variations in slope and porosity) for the four types. The water-retaining powers of the four soils are also different. Underground drainage is very different for the different soils, as is also the depth of permanent subterranean water, which is practically quite absent from two of the soils.

THE SOIL TYPES.—The geology and topography of the Tumamoc area are thoroughly described by TOLMAN in the monograph of SPALDING above cited. Tumamoc Hill, on which the Desert Laboratory stands, rises abruptly from the broad valley of the Santa Cruz River. The valley floor slopes very gently from the base of the hill to the river floodplain and to the various "washes," tributaries of the main river channel. The four soils here considered

may be briefly described as follows. A more complete description is included in the author's article above cited.

1. The soil of Tumamoc Hill is a heavy clay, underlaid by practically impervious rock at a depth of but 10–50 cm., and much broken into small pockets and irregular masses by outcropping rock or large rock fragments. Fully 50 per cent of the entire gross volume of the soil is made up of large and small rock masses. A subterranean water table does not exist here, so far as is known, and, from the impermeability of the underlying rock both to water and to plant roots, it is safe to conclude that the water supply for this soil is derived exclusively from precipitation. The unsifted soil possesses a water-holding power of 48 per cent of its dry weight. The usually pronounced slope of the soil surface here is partially offset by the numerous small catchbasins formed by rock fragments, so that rain water stands in small pools over the hill and does not drain away quite so rapidly as though the surface were more even.

2. The soil of the *Larrea* slope, so named from the prevalence of the creosote bush thereon, occupies the gentle slope which surrounds the hill. This soil is underlaid at a depth of 20–30 cm. by the limestone hardpan (caliche) so common in this region. The surface soil is more loamy than that of the hill, with an admixture of about half its volume of fine angular gravel; that near the caliche contains even more gravel and rock fragments, sometimes rounded pebbles. The slope, the smoothness and impermeability of the hardpan, the presence of rock fragments, and the loamy nature of the soil itself, all tend to make this a very well-drained soil. It, like the hill soil, is not influenced by subterranean influx of water. Unsifted soil from near the surface possesses a water-holding power of only about 20 per cent. This low retaining power is not here due to general coarseness of the soil, but to the large proportion of angular gravel, which of course holds practically no water.

3. The soils of the wash, a broad streamway from the Tucson mountains, which cuts through the general valley floor (*Larrea* slope in this vicinity) near the northern base of the hill, vary from gravel through sand to very loamy sand. The coarser soils are practically without vegetation and are of little interest in this

connection. The loamy sand, constituting little floodplains on the margins of the actual streamway, is 30 cm. or more in depth and is underlaid by coarser material. This is the soil here considered. It is practically without gravel admixture and has a water-holding power of about 25 per cent of its dry weight. It is almost certain (but without direct evidence) that an underground water table is present here, at least for many months of the year. The soil surface is nearly level and water is received from the superficial run-off of the hill and *Larrea* slope; however, it is well drained below.

4. The soil mass of the river floodplain, now completely abandoned by the stream, is of unknown depth. The surface layer is level and composed of clay loam with a water-holding power of about 39 per cent of its dry weight. This is about 8–9 meters deep and rests on sands and gravels, permanent water being met with at a depth of 10–15 meters. This soil is characterized by general absence of surface run-off and by but slow percolation to lower layers. The dry soil of the deeper layers, however, removes moisture from near the surface as rapidly as it can move downward by capillary action.

THE PLANT SOCIETIES.—The plant societies of the area about the Desert Laboratory have been thoroughly described by SPALDING in the work already mentioned, and also in a journal article (2). THORNBER'S ecologically classified list of species for this region (pp. 103–112 of the same monograph) is of especially great value to the student of environmental factors. The four types of vegetation which occupy respectively the four soil types here considered may be briefly characterized as follows:

1. The *Parkinsonia* society of Tumamoc Hill possesses more forms, both woody and non-woody, than any other of the four societies here considered. Besides this form of palo verde (*Parkinsonia microphylla*), the group includes the giant cactus (*Cereus giganteus*), the ocotillo (*Fouquieria splendens*), the barrel cactus (*Echinocactus Wislizeni*), several opuntias of both cylindrical and flat-stemmed types, *Acacia constricta*, *Larrea tridentata*, *Celtis pallida*, small specimens of mesquite, etc. *Bigelovia Hartwegii* occurs here but does not attain as great numbers or as large size as on the

river plain, where it is more characteristic. Numerous low forms are active throughout the year, notably *Encelia farinosa*, *Sphaeralcea pedata*, etc., and a great array of summer and winter forms are to be found at the proper season.

2. The *Larrea* society of the gravelly slope exhibits, in many localities, almost no woody species other than the creosote bush (*Larrea tridentata*). The bushes are uniformly and openly distributed over a surface which is otherwise nearly bare of vegetation, excepting during early spring and late summer, when numerous low forms appear. Of the desert shrubs within its climatic range, *Larrea* seems best fitted to withstand prolonged drought both of air and soil. *Ephedra* occurs upon the slope as well as in the wash, but makes its best growth in the latter place.

3. The *Cercidium torreanum* society of the wash is characterized by this form of palo verde and by mesquite (*Prosopis*), *Condalia lycioides*, and *Acacia Greggii*. The three latter forms are also characteristic of the *Prosopis* society of the plain. *Ephedra trifurca* and the creosote bush (*Larrea tridentata*) attain here their most luxuriant growth, though the latter, at least, is most characteristic of the *Larrea* society. Aside from these and some other woody plants, the vegetation of the wash consists mainly of small forms, which are active only during the periods of moist soil, either in winter or summer or at both seasons.

4. The *Prosopis* society of the river plain is dominated by mesquite, two forms of *Acacia* (*A. constricta* and *A. Greggii*). and *Condalia lycioides*. Annuals of many forms are numerous during the moist periods. The most striking of the low perennials is *Bigelovia Hartwegii*, which scarcely occurs outside this group, except for scattered plants in the *Parkinsonia* society.

METHODS OF DETERMINING AND OF REPRESENTING SOIL CONDITIONS.—The method used in determining the water-holding powers given above was to place the soil in a sheet-metal cylinder about 12 cm. high and 10 cm. in diameter, with perforated bottom (the latter covered externally with thin cloth), then to saturate the soil by standing in a vessel of water, at the same time pouring water on the soil surface, and finally to allow the soil mass to drain till no more liquid water came away below. From the weight of the

dry and saturated soil the water-retaining power is calculated in the usual way (3).

The actual soil moisture content was determined by the weighing and drying method, the temperature of drying being 105–110° C. The samples were taken, by digging, at depths of 15 and 30 cm. for all soils but that of the *Larrea* slope. For the latter soil, on account of its shallowness, the depths were 10 and 20 cm. Samples for each soil type were taken from the same area of a few square meters, the small excavations being immediately refilled. No later sample was taken from within 50 cm. of the soil thus disturbed. On December 13 irrigation water made it necessary slightly to change the position of the station for the soil of the floodplain, otherwise the stations remained the same throughout the whole period. Samples were taken at intervals of about 10 days. Three samplings were omitted for all soils during the month of June 1908. A few other omissions of single samples occur.

The specific gravities of these fours soils are approximately the same, there being almost no content of organic matter. Therefore the moisture contents are calculated on the basis of the dry weight of the soil and are here approximately comparable.

The careful work of Mr. J. C. BLUMER, Mr. E. E. SHERFF, and Professor J. E. KIRKWOOD, who performed the operations of collecting, weighing, and drying the soil samples, as well as that of keeping the rain record, is here gratefully acknowledged.

The accompanying graphs (figs. 1–4) have been constructed for each soil separately; the lesser depth is represented by a thin line and the greater by a heavy line. The precipitation record was kept for the hill station alone, but there is no reason to doubt that the rain record for the other stations would have been essentially the same had it been actually taken. For easy comparison, the rainfall is represented below the graphs of soil moisture simply by vertical, shaded blocks, the length of each block denoting the relative amount of precipitation which took place during the corresponding ten-day period. The figures directly above these blocks denote the precipitation in centimeters, that is, the relative length of the blocks. The data from which the moisture graphs are constructed are placed upon the figures directly above the base

TUMAMOC HILL
15 CM. DEPTH
30 CM DEPTH
30%
20%
10%
RAINFALL
IN CM.
OCT
NOV.
DEC.
JAN.'08
FEB
MAR
APR.
MAY
JUNE
JULY
AUG.
SEPT.
OCT
NOV.
DEC.
JAN.'09
FEB.

FIG. 1

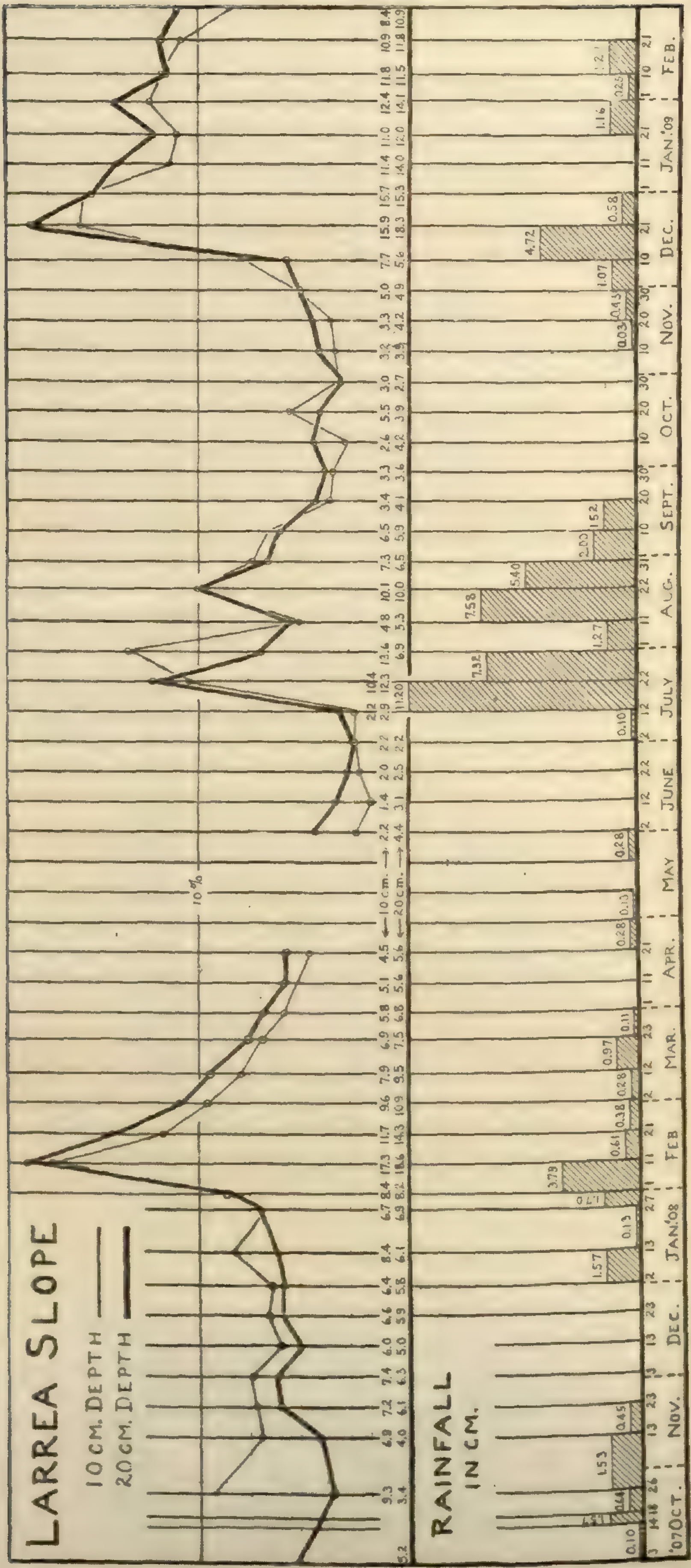
LARREA SLOPE
10 CM. DEPTH
20 CM. DEPTH
RAINFALL
IN CM.
10 %
← 10 cm.
← 20 cm.
JAN.'08
FEB.
MAR.
APR.
MAY
JUNE
JULY
AUG.
SEPT.
OCT.
NOV.
DEC.
JAN.'09
FEB.

FIG. 2

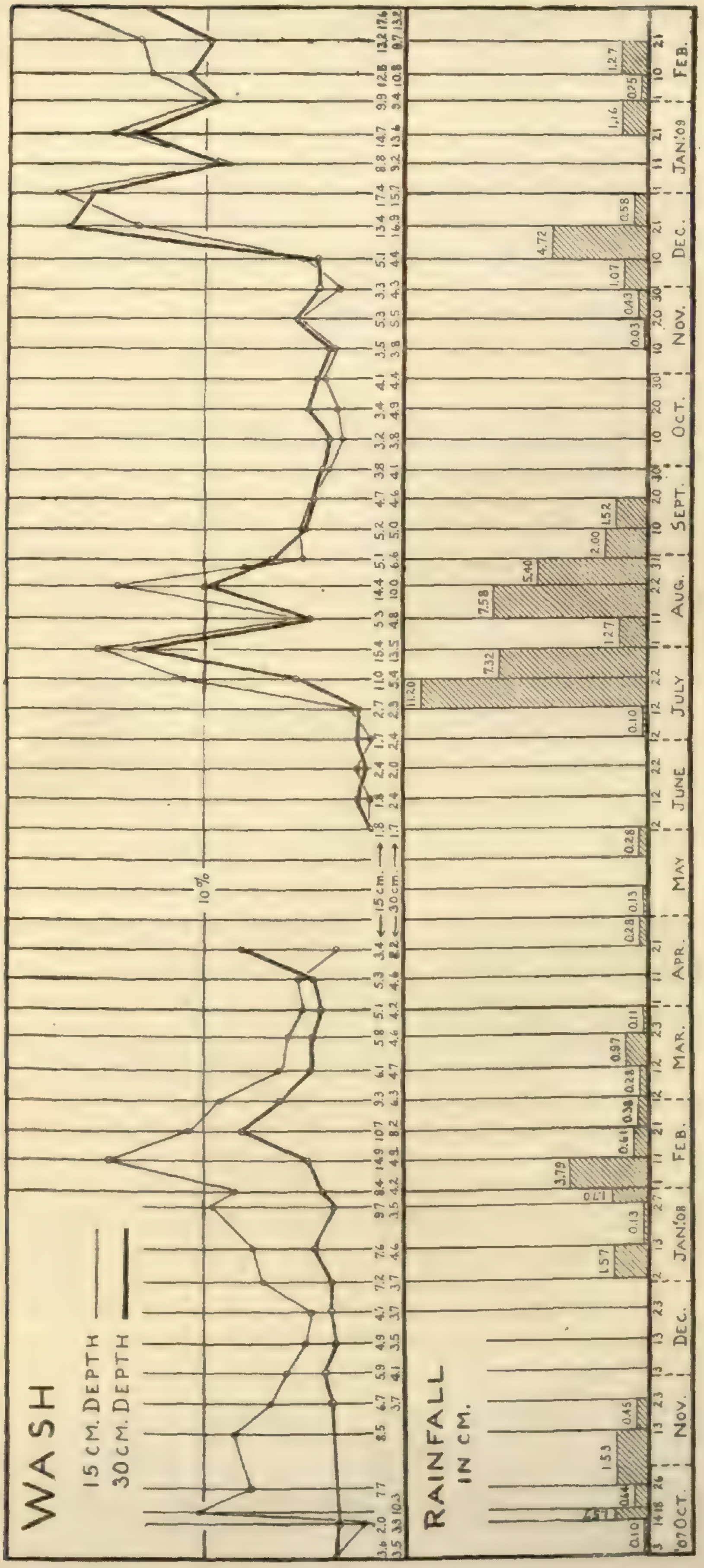
WASH
15 CM. DEPTH
30 CM. DEPTH
10%
15 cm. ⟵
30 cm. ⟵
RAINFALL
IN CM.
JULY
AUG.
SEPT.
OCT.
NOV.
DEC.
JAN.'09
FEB.
MAR.
APR.
MAY
JUNE
JULY
AUG.
SEPT.
OCT.
NOV.
DEC.
JAN.'09
FEB.

FIG. 3

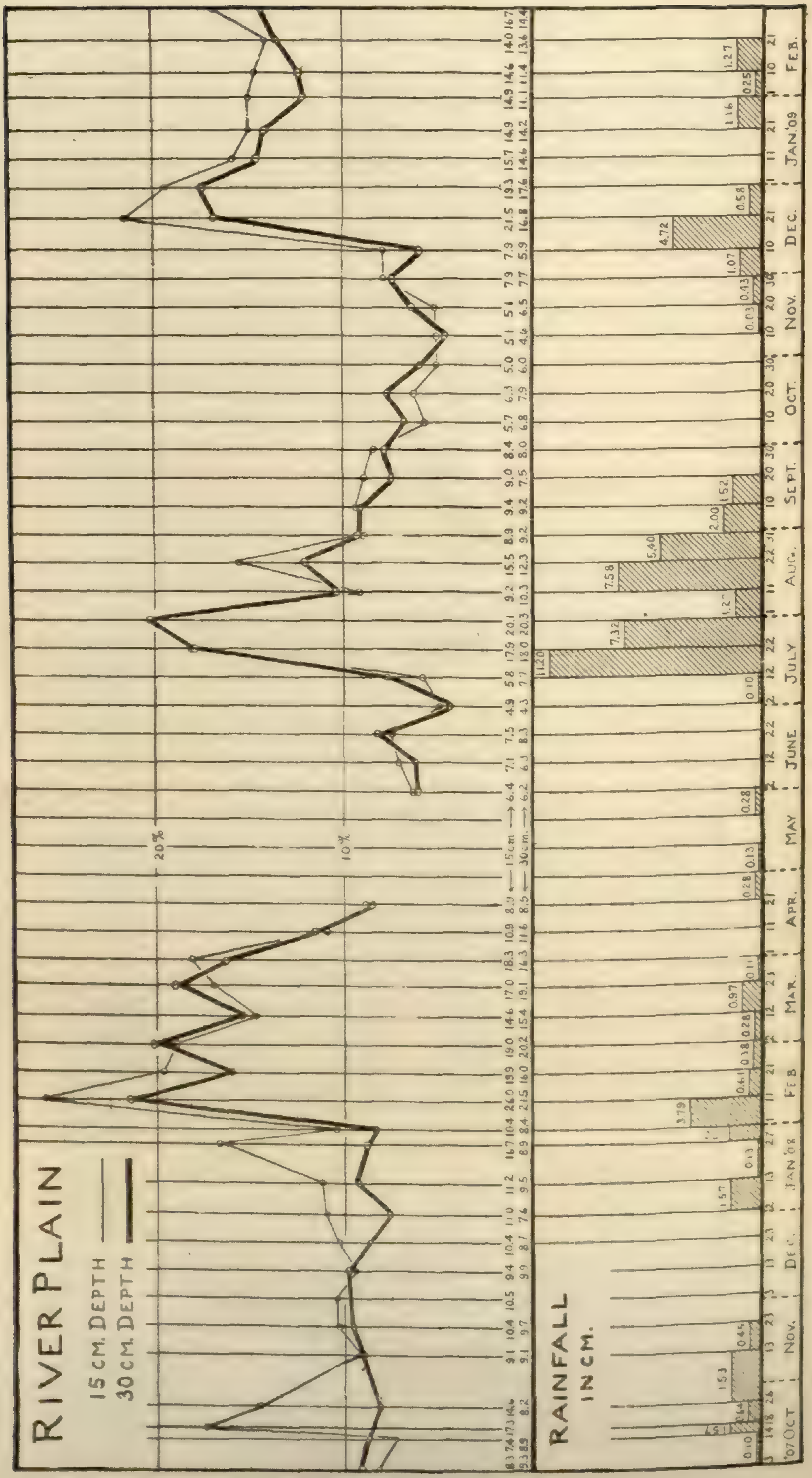
RIVER PLAIN
15 CM. DEPTH
30 CM. DEPTH
20%
10%
RAINFALL
IN CM.
JULY
AUG.
SEPT.
OCT.
NOV.
DEC.
JAN.'09
FEB.
MAR.
APR.
MAY
JUNE

FIG. 4

line of these graphs. They express percentage of dry weight. At the base of each figure, the dates of sampling are indicated. The major portion of the calculations and of the drawing of the graphs are the work of GRACE J. LIVINGSTON.

DISCUSSION OF GRAPHS.—It is to be remembered that several simultaneous samples at the same station would be expected to vary to some extent, especially in the stony soil of the hill and of the deeper layer of the slope. Therefore it is not surprising to note minor fluctuations in the graphs, which do not appear traceable to conditions of precipitation.

The graphs bring out clearly the lagging of soil moisture behind precipitation; it requires considerable time for rain water to reach the upper level of sampling and a still longer time for it to reach the lower level. A slight precipitation may not alter the condition of the soil at either level, the water being lost by evaporation before it can penetrate even to a depth of 10 or 15 cm. It also occurs that a rain which is only sufficient to moisten the surface layers, thus placing them in capillary connection with the deeper ones which are already moist, may actually accelerate the drying out of the deeper layers. Thus a slight rain is sometimes directly deleterious to the vegetation; it removes the dry mulch from the surface and fails to add markedly, if at all, to the deeper moisture content, so that before the dry mulch can regenerate, the deeper soil has lost considerable water by upward movement and evaporation.

From data given in *Publication 50* of the Carnegie Institution (pp. 66, 67) it appears that a number of plants of the hill, when grown in pots (in hill soil), wilted with a soil moisture content of 6–12 per cent by wet volume. On the basis of dry weight these numbers become about 7 per cent and 14 per cent. *Boerhavia* (one of the summer annuals of the hill) wilted in the open soil with a moisture content of 6–7 per cent by wet volume, or about 7–8 per cent on the basis of dry weight. These observations were taken in July and August, the period of the summer rains, when the evaporating power of the air was far below its magnitude of May and June or of October and November. With greater evaporation rate, the plants should of course wilt with a correspondingly higher soil moisture content. It is probably safe to assume, there-

fore, that during the driest months of the year the majority of the plants of the hill require an amount of soil moisture of 8–10 per cent. With a drier soil than this it is probable that most forms without pronounced storage organs would succumb in a few weeks.

No determination of wilting points is as yet available for the other three soils, but from the well-known fact that the "non-available water" in soils decreases, in general, with their water-holding power, it is probably safe to assume that vegetation can withstand a considerably drier soil in the case of the slope and wash, and a somewhat drier one in the case of the river plain.

From the graphs it is evident that the period of most intense drought occurs just before the beginning of the summer rains. In general, the month of June may be taken as the month of driest soils, and it is also the month of greatest evaporation. Therefore, for plants without well-developed water storage tissues, this month must approximate the critical period of the year so far as the water relation is concerned. It will therefore be instructive to derive the average soil moisture content for this month in the case of each of the four soil types. So far as I am aware, the root systems of all plants of this area, which are without storage tissues and which are not annuals, penetrate into the soil at least to the greater of the two depths here considered. We may therefore consider the greater depth alone. The following table presents these averages for the four determinations taken from June 2 to July 2, 1908. The water-holding capacities are also given, and the water content as percentage of the latter.

SOIL MOISTURE AT THE CRITICAL PERIOD

Soil type	Water-holding power, in percentage of dry weight	Average moisture content, June 1908		
		Depth in cm.	Percentage of dry weight	Percentage of water holding power
Hill	48	30	10.9	22.7
Slope	20	20	3.1	15.5
Wash	25	30	2.1	8.4
Plain	39	30	6.3	16.1

That the vegetation of the hill is the most varied and the most perennially active of all the plant societies of our area, agrees well

with the high soil moisture content (almost 11 per cent) and the high percentage of the moisture-retaining power (almost 23 per cent) which this soil exhibits during the driest month of the year. It is to be remembered in this connection that the soil of the hill is often considerably over 30 cm. in depth, and that, in the dry season, the highest moisture content is to be expected just above the underlying rock surface. In the summer of 1904, immediately preceding the advent of the July rains, a soil sample from a depth of 35 cm. on the hill exhibited a moisture content of 17.9 per cent of its dry weight. From the graph of the hill soil and from this last consideration may be derived convincing additional evidence in favor of the conclusion expressed by SPALDING and by the author (*Publication 50*, Carnegie Inst., p. 12) "that sufficient moisture is probably at all times present in the deeper layers of these soils [of the hill] for the needs of transpiration and even growth." The excellent soil conditions exhibited by Tumamoc Hill are emphasized by the fact that at no time during the period of record did the observed moisture content at a depth of 30 cm. fall below 8.9 per cent, and that it was far above 11 per cent at all times excepting in the months of June and November 1908.

The soil of the *Larrea* slope, at a depth of 20 cm., just above the caliche hardpan, exhibited only 3.1 per cent of moisture as the June average. Had the soil been sifted, the moisture content would undoubtedly have been markedly greater, as is indicated by the high percentage of its retaining power (15.5 per cent) which the moisture content represents. But the amount of water available for plants must be considered as a vanishing quantity at this time.

In this vicinity, practically the only perennially active plant on the slope, excepting a few scattered cacti and here and there a plant of *Fouquieria* (itself hardly perennially active), is the creosote bush, from which the slope is named. This plant, as has been mentioned, is probably the most resistant to drought conditions of all non-storage forms in the region. An inspection of the graph for this soil brings out the fact that the moisture content rose above 10 per cent only in February and March, in July and August 1908, and in the winter of 1909. In distinct opposition to the soil

of the hill, this soil is undoubtedly deficient in moisture for by far the greater part of the year. It usually supports spring and summer annuals for a few weeks during each of its moist periods.

The soil of the wash shows an even more inadequate moisture supply for the month of June than does that of the slope. This soil contains practically no gravel in its superficial layers and its moisture content at this time (2.1 per cent by dry weight) was only 8.4 per cent of its water-holding power. From the general aspect of the vegetation it would be concluded that this soil was better supplied with moisture than that of the slope, but the graph fails to explain this view. The discrepancy is apparently due mainly to the great depth of the soil, which acts as a much more extensive reservoir for water than the shallow soils of hill and slope. The presence of underground water is doubtless effective in case of those trees and shrubs the roots of which penetrate deeply. The continuously active forms which occur here must be considered as much more deeply rooted than is possible on the hill and on the slope.

The soil of the river plain exhibits a much more favorable moisture condition, not only in June, but throughout the year, than any other of our four soil types excepting that of the hill. Its average water content for the drought period was 6.3 per cent by dry weight. In terms of its moisture-holding power, this becomes 16.1 per cent. This is a deep soil, with unknown, but surely considerable, amounts of moisture below the limits of sampling. It also has constant subterranean water at depths which can probably be reached by tree roots. This latter fact seems to explain the occurrence here of mesquite, acacia, and other deep-rooting shrubs. In the dry seasons (early summer and late autumn) this soil shows very few active plants besides those just mentioned, but in the rainy seasons it supports a dense growth of annuals, being apparently as well suited to such forms as is the soil of the hill itself. That many annuals of the hill fail generally to appear on the plain, and conversely, is perhaps to be explained by the considerably higher moisture content occurring during the rainy seasons on the former soil. It may also be related to conditions which hinder surface

evaporation on the hill, such as the presence of numerous rock fragments on or in the soil.

An interesting question is suggested by the fact that the creosote bush dominates the slope and occurs on the hill, but is almost entirely absent from the plain, excepting along the margin where it abuts against the slope. No evidence as to why this shrub should not thrive on the plain is as yet at hand. The most vigorous specimens of the area occur along the lower margins of the slope, which agrees with a similar behavior always observed in irrigated specimens, in seeming to indicate that a more adequate water supply produces an abnormally great growth. SPALDING mentions the physiographical relation (which of course cannot *directly* affect the vegetation) that *Larrea* usually dominates gentle slopes which are being eroded at the present time. It would seem that there must be some condition in the soil of the plain which is antagonistic to the growth of this shrub. A study of the oxygen conditions of these soils may possibly throw some light on the subject. The moisture condition alone is inadequate to explain the facts.

The results obtained from a study of the graphs would place the hill soil first, as the best suited for general plant activities; the soil of the plain would occupy second place, and the two other soils would lie rather close together and far below either of these. This general arrangement agrees well with the vegetational characters of the four soil types if we consider that the deep-rooting forms of wash and plain obtain moisture from levels deeper than those here considered. It is also in fair agreement with the simple series of the water-retaining powers of the four soils. From this retaining power alone the soils would have been interpreted in the same general way. This emphasizes the water-holding power as an easily obtained and very important factor in studies of distribution.

The last-named factor has been used by the writer (4) with some success in a search for the determining conditions of forest distribution in Michigan. It appears that for different upland habitats of the same region, where the level of underground water is far from the surface, and the precipitation and evaporating power

of the air are approximately uniform, the relative soil moisture conditions may be fairly well approximated by the criterion of water-holding power. The ease of obtaining comparative data for this factor entitles it to a thorough test as a soil criterion for habitat studies.

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BALTIMORE, MD.

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THE EFFECT OF LONGITUDINAL COMPRESSION UPON THE PRODUCTION OF MECHANICAL TISSUE IN STEMS

L. H. PENNINGTON

(WITH TWO FIGURES)

Introduction

For more than a century observations and experiments have been made to determine what factors cause or influence the production of mechanical tissue in plants. Previous to PFEFFER's time, the causes were supposed to be of a mechanical nature. These explanations have been shown to be inadequate.[1] PFEFFER (**26, 27**) showed that tension, pressure, or even contact may act as a stimulus to cause the production of more mechanical tissue. NEWCOMBE (**21**) suggested that plants must respond to stress in a self-regulatory manner by producing mechanical tissue where it is most needed. He also indicated the complex notion in regard to stress, and suggested that it should be subdivided. At present we use the terms tension or traction, and pressure or compression, to indicate two opposite kinds of stress

To determine the effect of each kind of stress, much careful experimentation is necessary. HEGLER (**12**), BALL (**1**), HIBBARD (**14**), and BORDNER (**2**) have investigated the influence of tension upon growing cells, with regard to its mechanical as well as to its stimulatory effects. Although these investigators did not agree in all points, their results show that tension alone cannot cause a very marked increase in mechanical strength. VÖCHTING (**34**), HIBBARD (**14**), and BÜCHER (**4**) have contributed a little concerning the effects of longitudinal compression.

VÖCHTING reported that he fastened weights upon the tops of sunflower stems, some of which had been decapitated, and upon Savoy cabbages, all of which had been decapitated. After leaving the plants thus weighted for several months, he was able to discover

[1] For historical account see URSPRUNG, Biol. Centralbl. 1906.

no increase of mechanical tissue in the sunflower stems, and but a slight increase in the cabbage stems, an increase not at all proportional to the weights used.

HIBBARD suspended weights upon the stems of the sunflower, periwinkle, fuchsia, and coleus, and found in all except coleus a slight response to compression by self-regulatory increase in mechanical tissue. He did not believe, however, that the evidence could be regarded as conclusive.

BÜCHER inclosed both the upper and the lower portions of stems of the castor oil plant in plaster casts, and then fastened these casts so that the stems as they elongated were subjected to a longitudinal compression. All but two of his plants became bent; the two which remained straight were weaker in mechanical tissue than normal plants.

From the few data which have been recorded, it is very plain that we do not have sufficient evidence to show whether or not compression or increased weight may act as a stimulus to cause the production of a greater amount of mechanical tissue in plant stems. General conclusions have been drawn from mere observations of phenomena, which may be due to any one of several influences or to the combination of two or more influences. The few experimental data have led to indefinite or contradictory conclusions. This investigation was undertaken to secure exact experimental data upon the effect of weight tending to produce a longitudinal compression in vertical stems.

Materials and methods

PLANTS USED

From the nature of the experiments, it was necessary to use plants with single upright stems. Both woody and herbaceous plants were used. The woody plants were both one-year-old shoots and seedlings of the common locust (*Robinia Pseudo-Acacia*), both young and one-year-old shoots of sumach (*Rhus glabra*), one-year-old shoots of the poplar (*Populus tremuloides*), and the castor oil plant (*Ricinus communis*). The herbaceous plants were the sunflower (*Helianthus annuus*), the broad or Windsor bean (*Vicia Faba*), and the common bean (*Phaseolus*

vulgaris). The experiments upon woody plants were conducted in the garden during the spring and summer; those upon herbaceous plants were conducted in the greenhouse during the winter and in the garden during the summer.

METHODS OF EXPERIMENTATION

After many preliminary trials, the methods given below were found to be most suitable. For methods other than these, descriptions are given in the account of the different experiments in which they were used. In general, a large series of plants of the same size and age and growing under the same external conditions was used for each experiment. The plants were numbered consecutively. The height and two diameters of each plant were measured, one diameter of the part to be under compression and the other of the part above the compressed region. In case a stem was not cylindrical, the average of the greatest and the least diameter was taken as the diameter of the stem at that place. Strong cords were then looped about each stem at a suitable distance above the ground to serve as an attachment for the weights. The stems were protected from mechanical injury by the cords by first wrapping pieces of soft cloth, commonly known as table matting, around each stem. Each stem was then firmly fastened in a vertical position by tying it to stakes, not in contact with the plant, so that it could not bend or sway, and yet could be restrained in no way except by the downward pull of the weights. Weights were then suspended upon half of the plants, while the other half were left to serve as controls. All plants in a series thus treated were under exactly the same conditions, except that the lower part of each experimental plant was subjected to a compression caused by the downward pull of the weights. If the plants were practically equal in size, alternate stems were weighted; but if they happened to be somewhat unequal, care was taken to see that the average size of the experimental plants was equal to the average size of the control plants. For every large experimental plant, an equally large control plant was chosen, and for every small experimental plant, an equally small control plant was chosen.

More weights were added from time to time according to the

condition of the several experiments. In some experiments the weights were light, scarcely exceeding the weight of the plants; in other experiments they were equal to many times the weight of the plants themselves. Great care was taken to see that the stems were not bent by the weights.

MECHANICAL TESTS

At the conclusion of each experiment, all the plants were measured in the same manner as at the beginning, and the stems taken

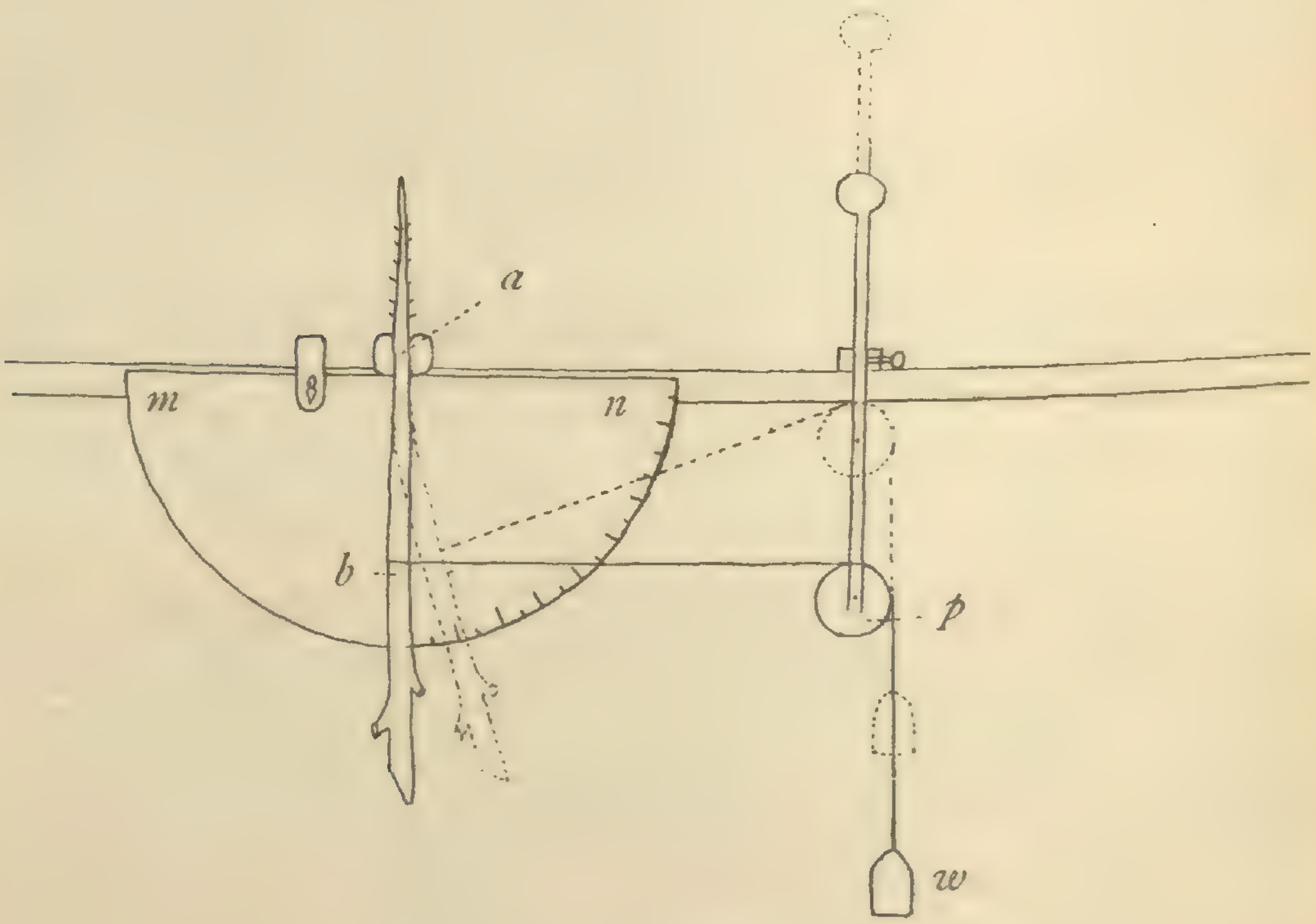

FIG. 1

to the laboratory for mechanical tests and anatomical study. The compressed part of each experimental plant, as well as the corresponding part of each control plant, was tested for rigidity, as shown by its resistance to bending, and for resistance to crushing.

The resistance to bending was determined by a simple piece of apparatus, which is represented by the diagram (fig. 1). The basal end of the stem to be tested was clamped securely at *a;* the cord was looped over the stem at *b*, always at a fixed distance from *a;* the weight *w* was then slowly released and the amount

of bending read in degrees upon the arc of the protractor *mn*. The testing weight for each series of plants was selected so that the plants would not be broken or too strongly bent. The pulley *p* could be adjusted as indicated by dotted lines, in order that the weight should at all times act in the direction perpendicular to the stem. This method was found to show very slight differences in the rigidity of stems.

The resistance to crushing was determined by the apparatus shown in fig. 2. A piece of the stem 10–15 mm. in length was placed with one end against the fixed block *f*, and the movable block *m* brought against the opposite end. The movable block was attached to the strong spring balance *s*, which in turn was attached

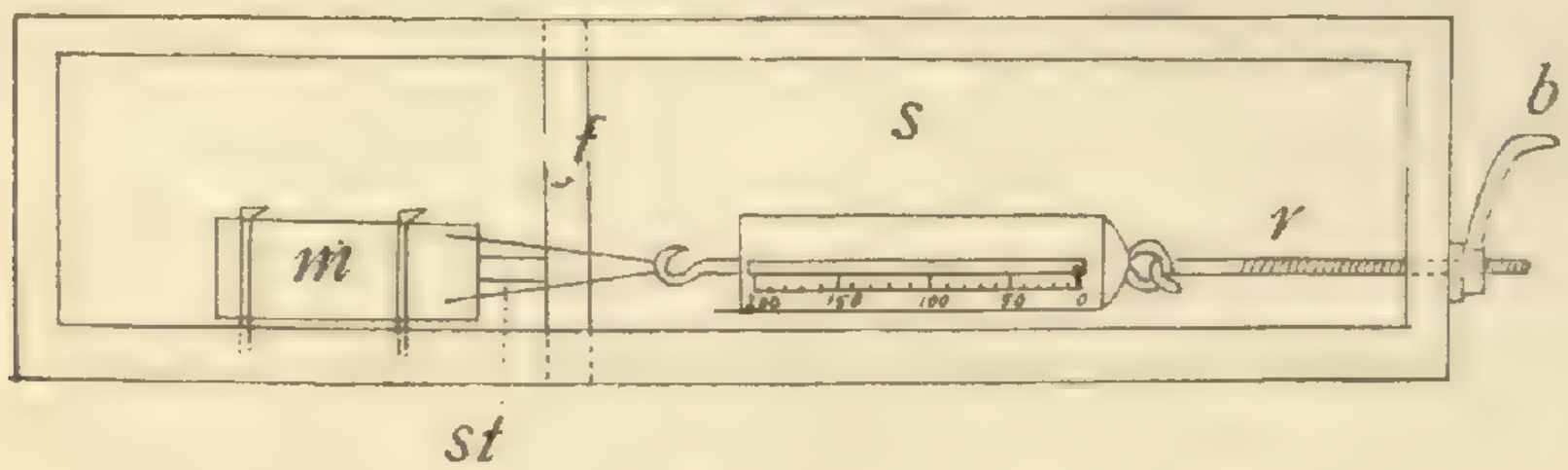

FIG. 2

to the threaded rod *r*. When the tail nut *b* was turned upon the rod *r*, the movable block *m* was drawn toward the fixed block *f*, thus subjecting the stem *st* to pressure. The amount of pressure could be read at once upon the scale of the balance. The resistance to crushing could be determined very sharply, for when the critical point was reached, the stem always gave way suddenly.

After testing a piece for resistance to crushing, the part of the stem next to that which was crushed was put into alcohol to be preserved for a study of the internal structure and microscopic measurements of the mechanical tissues.

ANATOMICAL STUDY

The anatomical studies and measurements were made from cross-sections, which were suitably prepared and stained so as to differentiate more clearly the various tissues, principally the xylem and hard bast. Chemical reactions (aniline sulfate with sulfuric acid, and phloroglucin with hydrochloric acid) as well as stains (acid fuchsin, aniline safranin, and methyl blue) were used.

The method which gave the best results and which was generally used was as follows: Cross-sections of uniform thickness were placed in watch glasses with a little 50 per cent alcohol and two or three drops of alcoholic safranin. In the course of three or four days, all the lignified cell walls were stained a bright red, while other tissues remained nearly colorless. The sections were then either washed in water and mounted in glycerin, or washed in 96 per cent alcohol, cleared in clove oil, and mounted in balsam.

Since xylem forms by far the greatest part of the strengthening, or mechanical, tissue, more measurements were made of this than of the other tissues. For this purpose, exact camera drawings of the lignified parts were made and the area of these drawings determined by means of a polar planimeter. Thickness of wall was determined by taking the average of several measurements, which were made by means of an eyepiece micrometer. Relative size of cells was determined by counting the number in a certain field in the microscope or by micrometer measurements.

In order to avoid the danger of a personal error in making the mechanical tests and microscopic measurements, the stems were numbered indiscriminately by a second person, so that the writer did not know which were experimental and which were control plants until after all tests and measurements were made and the results copied.

Experimental

COMMON LOCUST (ONE-YEAR-OLD PLANTS)

In April, before the growth had begun, 14 one-year-old plants were selected from a large number of sprouts. These plants were measured, tied securely to stakes, and weights suspended upon one-half of them. The cords about the stems were shifted from time to time to avoid constricting the stems as they increased in size. More weight was placed upon the experimental plants, from time to time, as long as they continued to grow. In October, when the experiment was concluded, some of the larger stems were supporting a weight of 20 kilos.

The results for this series of plants were not satisfactory in all respects. Several of the stems were broken or otherwise injured

during the summer. The growth was very unequal in different stems. Some of them increased in size three or four times as much as others, which grew under apparently the same conditions. This is not an uncommon occurrence, however, among shoots which spring from old roots.

Careful comparisons did not show any greater increase in growth or thickness of stem in the experimental plants than in control plants. On the other hand, some of the experimental stems had smaller diameters in the compressed portion than control stems. This diameter in three stems was less than the diameter of the same stem above the compressed part. Although this difference is normally not infrequently noticed in this species, it was rather more striking than usual in these plants. Cross-sections were prepared from experimental stems, control stems, and stems which had not even been tied to stakes. No differences, however, could be seen between any of them.

LOCUST SEEDLINGS

In order to obtain woody stems of more nearly uniform size, seedlings of locust were grown in the greenhouse and transplanted into the garden as soon as the weather became favorable in the spring. Of about 100 which were transplanted, only 30 were considered suitable for experimentation. These were prepared in the usual way and kept under experimental conditions until growth had ceased, about October 15. In the greenhouse, some of the seedlings grew to a height of 15–20 cm.; their stems, however, were very weak. When they were transplanted, they were bent nearly if not quite to the ground by every little breeze, which could scarcely bend locust sprouts which had come up in the garden. In two or three weeks' time, however, these slender seedlings, although they had grown but little in height, had become strong enough to withstand ordinary winds. Some of these slender seedlings were tied to stakes to prevent their being whipped about by the wind. Two or three weeks later, when the stakes were taken away, the plants were still unable to support themselves against a light wind.

This series was kept under the best conditions for growth. The plants were watered frequently during the dry season and protected

from all injury. The final measurements show that the plants grew well. The experimental plants increased 152 per cent in height, 131 per cent in the diameter of the weighted portion, and 122.5 per cent in the diameter a short distance above the weighted part; the control plants, in the same positions and dimensions, 142 per cent, 135 per cent, and 133.7 per cent respectively. The relative amounts of xylem for the experimental and the control plants were 95.17 and 100 respectively. Careful measurements of cell walls showed no difference between the experimental and the control plants.

SUMACH (ONE-YEAR-OLD PLANTS)

From a very large number of thrifty sumach sprouts 24 one-year-old plants were selected for experimentation. In April these plants were tied to stakes, and weights were placed upon the experimental plants in the usual manner. Conditions were fairly good during the growing season. The plants were kept under experimental conditions until October, although nearly all of the growth in size and thickness of stem took place in the spring and early summer. The final measurements and tests showed that the experimental and the control plants were practically equal in size and strength at the end of the season. A comparison of the actual increase in xylem, as determined from the annual rings, showed about 18 per cent less for the experimental than for the control plants. Careful examinations and measurements showed no difference in the size of cells or in the thickness of cell walls.

SUMACH (YOUNG PLANTS)

Sixteen young plants were placed under experimental conditions as soon as they had attained a height of about 35 cm. These plants did not increase greatly in size and thickness of stem. The tests and measurements showed that the strength and amount of xylem were very nearly equal for the experimental and the control plants. The percentage increase was somewhat greater for the experimental plants than for the controls. This difference, however, loses its significance when we observe that the actual increase in height was only 6.93 cm. for the experimental and 5.11 cm. for the control plants, and the increase in diameter only 2.07 mm. and 1.75 mm.

respectively. Careful microscopic examinations and measurements failed to show any differences in cells or cell walls.

POPLAR (ONE-YEAR-OLD PLANTS)

Sixteen plants of the poplar were selected and placed under experimental conditions in April. The plants were measured and carefully tied to stakes. Weights were suspended upon eight of the plants, and as the plants increased in size more weights were added. Although growth practically ceased in early summer, the plants were kept under experimental conditions until October.

The final measurements and tests showed no greater increase in the experimental plants than in the control plants; the increase, in fact, was somewhat less for the former than for the latter. For the experimental plants, the increase in height and diameter of the stem was less than 16 per cent, and for the controls 20 per cent; the relative increase in xylem 77 and 100 respectively; the resistance to bending 81 and 100 respectively. It is difficult to account for these differences. Although the conditions for growth were not good, owing to partial defoliation by insects, they were the same for both experimental and control plants.

CASTOR OIL PLANT (GREENHOUSE PLANTS)

Twenty-four plants of the castor oil plant were selected from a large number which were grown in the greenhouse. Before tying the plants to the stakes, the stems were carefully protected with pieces of table matting. Internodes of bamboo, about 10 cm. in length, were split in two and the halves bound upon opposite sides of each stem, the lower ends extending to within 5 cm. of the ground. Weights were suspended from the upper ends of these pieces of bamboo. In this way room was made for the weights to swing free from the ground, and the longitudinal pressure was confined to the lower 5 cm. of the stems. The plants were kept under experimental conditions for four weeks. The stems were 6 mm. in diameter and 15 cm. high at the beginning of the experiment; they increased about 50 per cent in diameter and 70 per cent in height during the experimental period. At the conclusion of the experiment, the experimental stems were under a pressure of about 1000 grams, equivalent to about 1.33 atmospheres.

The results of the final measurements and tests are shown by percentages. Assuming in reference to each measurement and test that 100 represents the value for the control plants, we have for the experimental plants the following numbers: height at the beginning of the experiment 97.67, at the conclusion 92.33; diameter at the beginning 100.2, at the conclusion 104.5; resistance to bending 120.6; resistance to crushing 104.2. The slightly greater bending and crushing resistances were probably due to the somewhat greater diameter of the experimental plants.

Cross-sections of the stems in this series were prepared and studied with special reference to the hard bast fibers and the collenchyma. The number of hard bast fibers in each stem was ascertained by counting. The average number for the experimental plants was practically equal to the average for the control plants. In each stem the thickness of three collenchyma walls was measured by means of an eyepiece micrometer, and from these measurements the average width of the collenchyma walls determined; there was found to be a difference of only 0.07 μ between the two averages; moreover, this excess was on the side of the control plants.

CASTOR OIL PLANT (GARDEN PLANTS)

Eighteen castor oil plants were selected from a large number grown in the garden. These plants were tied to stakes and weighted in the usual manner. They were about 17 cm. in height and 9.5 mm. in diameter at the beginning of the experiment; they increased about 75 per cent in height and 40 per cent in diameter during the experimental period of ten days. At the conclusion of the experiment, the experimental plants were supporting 5–7 kilos each. The usual measurement and test showed no marked differences. Letting 100 represent the value for each control plant average, the following numbers represent the relative values for experimental plant average: height at the beginning of the experiment 101.3, at the conclusion 97.2; diameter at the beginning 101.6, at the conclusion 101.4; resistance to bending 101.8, to crushing 107.5; amount of xylem 109.3.

Another experiment was conducted with 30 selected castor oil

plants, which were divided into three equal sets: experiment plants, control plants, and counterbalanced plants. Each stem of counterbalanced plants was not only tied to prevent bending, but relieved from supporting the weight of the plant itself by tying a cord about the stem, passing it up over a pulley, and attaching a weight to the free end; this weight was kept practically equal to the weight of the plant. These plants were about 20 cm. in height and 9 mm. in diameter at the beginning of the experiment; during the experimental period they increased about 40 per cent in height and 22 per cent in diameter. The growth was less in this experiment than in the former experiment because of more unfavorable weather conditions. The final measurements and tests showed no more marked differences than in other experiments.

SUNFLOWER (GREENHOUSE PLANTS)

From plants of the sunflower which were grown in pots in the greenhouse, 30 of those with straight stems of nearly uniform diameter were selected for experimentation. The stems for this experiment also were bound upon opposite sides with pieces of bamboo to localize the longitudinal compression in the lower portions. More weights were suspended upon the pieces of bamboo from time to time, until at the end of the experimental period of four weeks the experimental plants were supporting a weight of 230 grams each.

The stems were 3.5 mm. in diameter at the beginning and about 5.25 mm. at the conclusion of the experiment. Assuming that 100 represents the value of each measurement and test for the control plants, the following numbers represent the values for corresponding measurements and tests in the experimental plants: height at the beginning of the experiment 99.8, at the conclusion 97.4; diameter at the beginning 95.9, at the conclusion 98.4; resistance to bending 66.7, to crushing 93.5. These numbers show very clearly that there was no greater increase in the experimental than in the control plants. The test for resistance to bending especially showed less strength in the experimental than in the control plants.

Although the mechanical tests would seem to show conclusively

that no increase in mechanical tissue had been caused by weight or compression, cross-sections were prepared and careful examination made to determine the relative amounts of collenchyma, hard bast, and xylem. In none of these tissues could any difference be detected between the experimental and the control plants.

SUNFLOWER (GARDEN PLANTS)

Thirty sunflower plants were selected from a large number of plants and placed under experimental conditions in June. Longitudinal compression was confined to the lower part of the stems by using pieces of bamboo, as in former experiments. Conditions for growth were very favorable. The plants were about 15 cm. in height and 6 mm. in diameter at the beginning of the experiment; during the experimental period of nine days, they increased 100 per cent in height and 70 per cent in diameter. The weights, which were necessarily light at first, were increased daily until the average weight for each experimental plant was 1400 grams (about three atmospheres).

At the conclusion of the experiment the usual measurements and tests, with one exception, were made. Instead of determining the resistance to crushing in this series, the tensile breaking-strength was determined by means of BORDNER'S (2) apparatus. If we assume that 100 represents the value of each measurement and test for the control plants, the following numbers represent the values of corresponding measurements and tests for the experimental plants: height at the beginning of the experiment 105.5, at the conclusion 110.2; diameter at the beginning 94.1, at the conclusion 99.4; resistance to bending 80; tensile breaking-strength 64.2; amount of xylem 80.4. These numbers show that, although the amount of growth in both the experimental and control plants was practically equal, the gain in strength and in mechanical tissue was less in the former than in the latter. The heavy weights evidently retarded the production of mechanical tissue.

A second series of 24 somewhat older sunflower plants was placed under experimental conditions in the usual manner by tying the

plants to stakes and suspending weights upon half of the stems. The plants were 22 cm. in height and 8 mm. in diameter at the beginning of the experiment; they increased about 140 per cent in height and 50 per cent in diameter during the experimental period. The final measurements and tests showed very little difference between the experimental and the control plants.

A third series of 81 selected sunflower plants was divided into three sets and placed under experimental conditions. The first set consisted of 29 experimental plants, the second set of 29 control plants, and the third set of 23 control plants which were relieved from supporting their own weight by cords looped around the stems, passed over pulleys above the plants, and attached to weights, which were kept sufficiently heavy to counterbalance the weight of the stems. The plants in this series were about 38 cm. in height and 10 mm. in diameter, and were kept under experimental conditions ten days. During that time they increased 80 per cent in height and 35 per cent in diameter. Weights were added daily until each experimental plant supported 6–7 kilos.

The usual measurements and tests showed a very great similarity in every respect in all three sets. In no case was there a difference of more than 6.1 per cent between the averages for any two sets. The relative resistance to bending was as follows: experimental plants 106.1, control plants 100, counterbalanced controls 96.2. The relative amount of xylem was: experimental plants 103; control plants 100; counterbalanced controls 98.

WINDSOR BEAN (GREENHOUSE PLANTS)

Several experiments were conducted in the greenhouse with the Windsor bean. Experimental plants tied to stakes and with the longitudinal compression localized in the lower portion, control plants tied to stakes, counterbalanced controls, and plants which grew normally, without additional weight or support, were compared with reference to strength of stem and amount of mechanical tissue. In no case did additional weight or decreased weight seem to have any influence upon the plants. Stems of plants which had been tied to stakes were found to be slightly weaker than stems which had not been tied.

COMMON BEAN (GARDEN PLANTS)

Twenty-four plants of the common bean were selected and placed under experimental conditions. The longitudinal compression was localized in the lower parts of the stems by means of the pieces of bamboo. Measurements and comparisons showed no greater gain in mechanical tissue in the experimental plants than in the control plants.

Discussion

The question of growth and increase of mechanical tissue with special reference to compression may be considered under five heads: (1) heredity and variation; (2) correlation; (3) mechanical effects of compression; (4) stimulatory effects of compression; (5) compression in connection with other stimuli.

HEREDITY AND VARIATION

The production of a certain amount of mechanical tissue in plants is a specific characteristic just as much as is the production of leaves of certain form. Just as leaves of a given species may vary in number and size under the laws of fluctuating variability, so may the amount of mechanical tissue vary. Entirely independent of any known cause, sudden variations may occur in the amount of mechanical tissue formed. The best illustration of this sudden variability is furnished by *Oenothera lata* (De Vries 9), a mutant which does not produce enough mechanical tissue to support its own weight. Another common illustration is furnished by certain laciniate-leaved varieties of the sumach, which have stems too weak to bear their own weight. The difference in the amount of xylem in closely related forms is shown in many grafts. When a scion of one species of elm is grafted upon another species or variety, it soon becomes larger than the branch upon which it was grafted, although there is more mechanical strain upon the branch than upon the scion. The same phenomenon is frequently seen in grafts upon fruit trees.

All of my experiments, especially those in which the weight of the plants was counterbalanced, showed that it is characteristic of each of the species to produce a certain amount of mechanical

tissue. It may be that at some time in the history of a plant it was susceptible to mechanical stresses, and that as a result of these stresses the plant gradually came to develop normally a certain amount of mechanical tissue without regard to the stresses to which it might be subjected. Whether this is the case or not is a mere matter of speculation, so far as this work is concerned, since of course experiments can throw no light upon that phase of the problem. Yet some plants may still be able to respond in a slight degree to such stimuli. It was with this possibility in mind that such comparatively large numbers of plants were used and careful measurements made in order that individual variations might be obliterated in the average of a large number.

It is possible and even altogether probable that the importance of such differences and variations may not have been given the proper amount of attention, or that they may have been overlooked entirely. In this work, however, the possibility of an error from both specific and individual variation has been eliminated by getting the averages of a large number of the same species for each experiment. Further discussion of this phase of the question, therefore, may be omitted. Heredity, however, does have a very important bearing upon the problem in another way.

The ability to produce certain tissues may be hereditary but latent in a plant, and require a certain definite stimulus to make it appear. Many plants do not produce leaves unless they feel the stimulus of light; others, cacti for example, produce leaves only when deprived of light. The experiments of VON DERSCHAU (**35**) and WORGITZKY (**37**) show that mere contact may cause the production of a certain amount of mechanical tissue, and contact and strain together are necessary to cause a tendril to produce its normal amount of mechanical tissue. The results of my experiments show that, at least in the plants which were used in this work, no latent hereditary activity is brought forth by compression.

CORRELATION

Under this head may be considered all those observations upon the mechanical tissue in fruit-bearing stems and branches. DENNERT (**6**), REICHE (**29**), and PIETERS (**28**) found in the great num-

ber of instances which they investigated that anatomical changes resulting in greater strength go hand in hand with the development of the fruit. These changes have been attributed both to the strain which is caused by the weight of the developing fruit, and to greater growth activity which is due to the carrying of the greater amount of building material which the fruit demands. KELLER (16) affirmed, however, that the fruit-bearing axis is not strengthened by strain or fruit-bearing in itself, but that the bending of the stem from the orthotropic to the plagiotropic position causes the anatomical changes. It is evident that these observations cannot throw any light upon the stimulatory effect of a tension or a compression acting alone. An experiment by VÖCHTING (34), however, does have a more direct bearing upon the question. He found that by removing the flower buds he could greatly retard the development of the mechanical tissue; the plants were sunflowers and fruiting stems of the Savoy cabbage. He also found that by stress brought about by weighting he could not cause the mechanical elements to reappear (the discussion of this stress is taken up in another place), but when he grafted a scion upon a decapitated stem, the cambium at once began to form the mechanical elements again, although the weight of the scion was equal to only a fraction of the weights which he had placed upon similar plants without result. He sums up the results of his experiments in the following words:

> Aus dem mitgetheilten folgt, dass der ontogenetische Gang der Gewebedifferenzierung von inneren, correlativen Verhältnissen beherrscht, dass die Bildung der einzelnen Gewebeformen nicht einfach durch das Bedürfniss bestimmt wird. Die Auslösungs-Theorie genügt hier nicht.

This experiment shows very clearly that correlation may have much more to do with mechanical tissues than mere stress or strain.

Correlation is also seen in many trees in which one-sided growth in the wood is correlated with a greater development of the root system on that side, or with the greater number of branches and the correspondingly greater leaf surface of that side. KNY (17) asserted that one-sided leafing of a tree must be associated with one-sided increase in the growth of the trunk. HARTIG (10) reported that this is the most common cause of eccentric growth in

pine trunks, although there were exceptions to the general rule. WIESNER (**36**) has attempted to explain eccentric growth in branches by attributing it to unequal size and distribution of the leaves.

In accordance with the observations given above, it was found necessary to keep in mind constantly the correlation between the growth of mechanical tissue and the growth of other parts of the plant. Locust shoots, which at one time were apparently equal and growing under equal conditions, were found to develop at very unequal rates, apparently because of differences in the amount of nutriment stored in the roots from which the separate shoots had sprung.

The differences in herbaceous stems under different conditions are perhaps best illustrated by sunflowers which were grown in the greenhouse and plants of the same kind and age which were grown in the garden. The tall, slender greenhouse plants at the end of four weeks had such poorly developed xylem cylinders that many of the stems were not able to support the weight of the tops, while the garden plants in the same time had become strong and robust, with well-developed xylem cylinders. This is, of course, an extreme case. Many plants, however, which were grown under apparently the same conditions had to be rejected because of abnormalities or differences in growth. By selecting plants which were as nearly uniform as could be obtained, and by keeping all conditions of growth as nearly equal as possible, it was thought that accurate results could be obtained, especially since the possibility of a personal error was also excluded.

MECHANICAL EFFECTS OF COMPRESSION

The textbooks assert that pressure, or compression, retards growth and may completely stop it if the pressure is great enough (PEIRCE **24**, JOST **15**, PFEFFER **26**). It seems no more necessary to make this assertion than to assert that heat, for example, may retard growth or even kill the plant if the temperature be high enough. It is of importance, however, to know whether retardation is proportional to the pressure, and whether changes take place in the cell or in its walls.

The effect upon the plastic growing cell must be the same whether it is compressed or whether it meets resistance to further growth. There can also be no difference in the hydrostatic or the osmotic pressure within the cell, whether the pressure be in one direction or another. In stems a longitudinal pressure causes the cells to exert a greater lateral pressure upon each other, and *vice versa* a lateral pressure must cause them to exert a longitudinal pressure upon each other.

Earlier writers assumed that growth must be inversely proportional to the external pressure exerted upon the growing cells. According to this view, the greatest growth must be in the region of the least pressure. It was upon this assumption that DETLEFSEN (7), SACHS (30), NORDLINGER (23), and KNY (17) sought to explain the eccentric growth of stems and branches. They had then merely to account for a loosening of the bark in some way to cause increased growth. DE VRIES (8) would account for the annual rings by assuming that the bark pressure is greater at some seasons of the year than at other seasons. The experiments, in which he retarded growth and caused the production of smaller cells by putting ligaments around the trunk, showed that great pressure may retard growth, but his relieving pressure by cutting the bark with a knife produced traumatic effects and not true growth. KRABBE'S (18) experiments proved that these theories for unequal growth were erroneous, for he showed that the bark pressure is never great enough to retard growth. This was an indication that growth cannot be directly or indirectly proportional to the pressure. This point was still further emphasized and cleared up by PFEFFER (25). PFEFFER says also (*Plant Physiology* 2:125):

> When a root pushes an object in front of it, its rapidity of growth is not perceptibly affected unless the resistance offered is very great.

Although the living protoplasm must control in a large measure the manner in which the cell meets external compression. this subject is discussed under the head of mechanical effects rather than in connection with compression as a stimulus. The manner in which the cell meets external resistance is best told by PFEFFER (*op. cit.*, p. 124):

> Under such circumstances [when a plant part is compressed] the tension of the cell walls is gradually replaced by the external pressure, against which the whole osmotic pressure finally acts.

It is thus seen that the plant does not meet a compressing force by growth and cell division, but by osmotic pressure. In reference to growth activity in cells under compression, NOLL's (**22**) experiment seems very significant. He showed that in bent roots secondary roots do not arise from the concave side where the cells must be compressed.

HARTIG (**11**), CIESLAR (**5**), and SONNTAG (**31**) attributed the increased thickness of cell walls in heartwood to pressure. Now it does not seem reasonable to think that pressure could cause the walls to become thicker, unless it acts as a stimulus merely to cause greater protoplasmic activity. Since the plant opposes external compression, or resistance to growth, by its osmotic pressure, it would be detrimental to the plant to have the walls lignified before their limits of expansion had been reached. That secondary thickening does not take place until the extension of the cell wall has ceased seems to be the general rule. PFEFFER (*op. cit.*, p. 27) says:

> After the stretching growth of the cell has ceased, the cell wall commonly undergoes secondary thickening;

and again (*op. cit.*, p. 32):

> An intimate correlation exists between the different forms of growth, and the thickening, cuticularizing, or lignification of the cell wall usually take place when the external growth has ceased.

In regard to the part which the increase in thickness plays in overcoming resistance, we may again quote PFEFFER (*op. cit.*, p. 124):

> Even when external growth has ceased, the thickening of the cell walls may still further increase the pressure which the growing tissue is capable of exerting. The observed pressures, however, are *not* greater than could be produced by the osmotic pressure *alone*.

BÜCHER (**4**) found in his "kamptotrophic" and "geotrophic" stems that thickening of cell walls was always retarded in the parts of the stem which were under compression.

The best experimental evidence of the effect of pressure upon cell walls was given by NEWCOMBE (**20**). Plant stems were inclosed

within plaster casts; as they increased in diameter, the pressure became greater. It was found that under these conditions the cells remained alive and active, yet the walls remained thin. Even the walls which had already begun to thicken ceased to become thicker as pressure increased.

My experiments in which very young sunflower stems were subjected to heavy weights showed fairly well the retarding effect of a longitudinal compression, for the amount and the strength of the mechanical tissue was found to be less in the experimental than in the control plants.

THE STIMULATORY EFFECTS OF COMPRESSION

Very little is to be found in botanical literature upon longitudinal pressure, or compression, as a stimulus, and still less as to its effect or lack of effect upon mechanical tissues. In nearly every instance in which the stimulatory effect of pressure is mentioned, it is loosely applied or very evidently connected with other causes of stimulation. PFEFFER states (*op. cit.*, p. 124):

> Various stimulatory influences are exercised by tension, pressure, and mechanical vibrations or disturbances.

What he says concerning the influence of compression has already been discussed under mechanical effects.

In nearly all researches, compression has been associated with other stimulatory influences. Those observations in which the author attributed the observed effects to pressure, or compression, are discussed under this head.

HARTIG (**10**) found that trees which were subjected to the action of a west wind produced thicker annual rings upon the east side than upon the west side. His explanation is best given in his own words:

> Der Druck des Windes übt einen Reiz auf das Plasma der Cambiumschicht aus, welche in zweckentsprechender Weise durch gesteigertes Wachsthum und durch Dickwandigkeit der Organe auf diesen Reiz reagirt.

These observations have not been confirmed by experiment, and URSPRUNG (**32**) has shown by his observations and experiments that longitudinal compression cannot account for these phenomena.

CIESLAR (5) bent four young spruces at right angles so that the upper parts lay in a horizontal plane, and kept them bound in that position for two years. He found the greatest increase in the thickness of annual rings to be in the concave or compressed side. From this experiment he concluded that pressure causes the greater increase in growth. The objections to this conclusion, however, are obvious. CIESLAR apparently did not consider the tension upon the convex side, nor the one-sided effect of gravity, which must produce a geotropic influence as soon as the tree is bent from the perpendicular position. The same objections may also be made to SONNTAG'S (31) conclusions.

VÖCHTING'S (34) experiments, however, require more consideration. VÖCHTING'S report of his experiments leaves room to question whether his plants were placed under longitudinal compression, tension, or a combination of the two. After finding that sunflower and cabbage plants, which had been decapitated to prevent fruiting, did not produce the normal amount of mechanical tissue, he says:

Zunächst und vor allem fasste man die mechanischen Zellen in's Auge. Nach HEGLER'S bekannten Angaben kann man durch künstliche Belastung nicht nur eine raschere Entwickelung dieser Elemente herbeiführen, sondern ihre Neubildung sogar an Orten bewirken, an denen sie sonst nicht entstehen. Ist diese Angabe, die durch unsere eigenen Erfahrungen nach gewissern Richtung bestätigt wurde, richtig, dann darf man erwarten, dass die veränderten Objecte unseres Versuches, wenn künstlich belastet, die mechanischen Elemente wieder hervorbringen. Von dieser Voraussetzung ausgehend wurden am Blühen verhinderte Pflanzen des Wirsing und der Sonnenblume durch Gewichte belastet, die in geeigneter Weise am Scheitel angebracht waren; bei der zuletzt genannten Pflanze wurden ausserdem noch normal blühende Objecte zum Experimente verwandt. Die Belastung war verschieden gross; die grösste betrug bei der Sonnenblume 20 Kilo, beim Wirsing mehr als 6 Kilo, Gewichte, die das der Blüthen- und Fruchtstände, welche, unter gewöhnlichen Verhältnissen von der Pflanze erzeugt werden, um ein Vielfaches übertreffen. Die Belastung dauerte Monate lang.

If we understand by this that the writer had in mind HEGLER'S (13) experiments in which stems were subjected to tension or pull, we should take this "geeignete Weise" to mean that weights were fastened so as to exert a pull upon the stems. This is the interpretation placed upon it by BALL (1), HIBBARD (14), and BORDNER (2).

If, on the other hand, we take the meaning in the general sense, that a plant responds to the demands ("das Bedürfniss") made upon it, we may interpret the phrase to mean that he fastened the weights in such a way as to simulate the tension caused by the fruiting head. BÜCHER (4) interpreted this to mean a longitudinal pressure or compression, as indeed it must if the fruiting heads remained erect. Since, however, the fruiting head of a sunflower droops, it must exert tension upon the part of the stem next to it, and both tension and compression in the bent part, tension upon the upper or convex part and compression upon the under or concave part. It seems from a later statement of VÖCHTING'S that the stems were kept erect. In that case, the "Belastung" must have exerted a compression only. He says in summing up his results:

> Wir fanden, dass selbst sehr starke Belastung der *aufrechten* am Blühen verhinderten Objecte nicht genügt, um das normale Holzwachsthum wieder herbeizuführen.

BÜCHER found weaker development of the mechanical tissues and less cambial activity in the two castor oil plants which he subjected to longitudinal compression than in normal plants. The stems were also larger in diameter, owing to the abnormally large thin-walled cells.

HIBBARD (14) used the same general method for subjecting stems to compression that I have employed in this investigation. His experiments were of a preliminary nature, comparatively few plants were used, and there is no record of his making mechanical tests or exact measurements of the mechanical tissue. When so few plants are used and no averages made, errors from individual variation may easily occur. It is not certain that the possibility of personal error was eliminated, although he says that the same conclusions were arrived at by two persons working independently.

In reference to HIBBARD'S experiments as well as to my own, a question may arise as to whether a stimulus is really exerted by such means as were used. This question may be answered in several ways. It is well known that living protoplasm is very sensitive. This sensitiveness is shown by the responses of *Mimosa*

leaves and by tendrils. The researches of BOSE (3) have shown that the protoplasm of other plants and plant parts is equally sensitive, although the plant cannot respond by a perceptible movement. In case growth is retarded, as it was in some of the experiments, the protoplasm must necessarily feel the effect. It has been demonstrated that there are interacting stresses in plants, of which a good example is afforded by twisted tree trunks. Force is required to cause such a twisting. If the weight of the top is the force, twisting must be accompanied by a shortening of the central cylinder or by an elongation of the outer layers. In either case, a longitudinal compression must be exerted upon the outer cells. It is not certain that the inner cylinder may become shorter, but it has been shown that wood cells may increase in length from the center to the circumference of a tree trunk. If this elongation of cells tends to lengthen the outer layers of wood in straight trunks, increased weight upon the trunk must alter the internal equilibrium of stresses, for it not only acts directly upon the outer layer, but it tends to increase the retarding action of the inner cylinder. Moreover, it is not safe to say that the woody cylinder is so rigid that it cannot change, for we know that wood is more or less elastic, and that the limit of elasticity may be exceeded by either great pressure or great tension. If a bar of wood is forcibly bent and kept in that position for some time, a readjustment takes place so that the bar remains bent without the external force. The sensitive protoplasm in a cambium layer, which surrounds closely a cylinder of wood, must feel very slight changes that might occur in the cylinder.

If the weight of the plant can furnish a stimulus for production of increased mechanical tissue, this stimulus must be lacking when the stem is relieved from supporting the weight of the plant. For the same reason an increased weight, equal to two, four, ten, or twenty times the weight of the plant, ought to produce a response by an increase in the strengthening tissue. Assuming that plants do respond to various stresses by becoming stronger, and that they remain weak if relieved of all stress, then the plants used in my experiments were placed under the most favorable conditions to respond to a given stress, for they were relieved of all stress except

the downward pull of the weights. In no case, however, were they found to become stronger mechanically. It must be concluded that a longitudinal compression, acting by itself and acting continuously upon a plant stem, cannot stimulate it to greater activity, nor to an increased strengthening of the tissues that are already present.

COMPRESSION IN RELATION TO OTHER STIMULI

For convenience, we may separate the stimulatory influences into three groups: the so-called internal stimuli, environmental stimuli, and strains or stresses. These internal stimuli may be due indirectly to environmental conditions. Since we know little or nothing about them, it is convenient to refer to this group all those phenomena which we cannot attribute to definite external conditions or stimuli. Environmental stimuli include gravity, light, heat, moisture, etc. Strains or stresses are tension and compression.

In nature the various influences are intimately associated with each other, and often so modify one another that observers and sometimes experimenters have overlooked certain influences and thus given undue weight to others. As an example we may speak of HARTIG'S observations and CIESLAR'S experiments in which pressure only was considered, where evidently gravity, tension, and perhaps other influences may have played an important part.

Others, who were not able to account for observed phenomena by certain external stimuli, explained them by saying that they are due to internal stimuli. As an illustration, a quotation from MASSART (**19**) will serve very well. In speaking of root swellings and eccentric growth in *Ficus* roots he says:

> L'épaississement asymétrique est régi par la gravitation, par la lumière et par des excitants internes, encore indeterminés.

Experimenters who examine more closely into the reactions of plants are forced more and more to the conclusion that the plant acts as a unit in a self-regulatory manner to bring about the greatest good to itself. NEWCOMBE (**21**) was the first to point out the necessity of considering the self-regulatory power of plants with special reference to their response to stress. URSPRUNG (**32, 33**) came to practically the same conclusion after a series of observations upon eccentric growth in trunks and branches.

BÜCHER (4) also arrived at this conclusion as a result of trying to bring his results into harmony with BALL'S (1) conclusions.

The application of the self-regulatory theory may seem to serve merely as a term to cover our ignorance. In reality it throws much light upon the whole question of stimulatory reactions, since it shows the great number of possibilities. In order to determine the influence of one factor, all the others must be taken into consideration, and their influence either eliminated or equalized by the use of both experimental and control plants under exact experimental conditions.

Considerable investigation has been carried on with respect to the various environmental stimuli. Further discussion of them, however, is not necessary in this place. In regard to the stimulatory effect of stresses and strains, comparatively few exact data have been obtained.

If we consider BORDNER'S results in regard to tension, it seems that a little more definite conclusion may be drawn from BÜCHER'S, as well as from my own experiments. BÜCHER found that when a stem is bent and then placed upon a klinostat the cell walls on the convex or tension side become thicker, and on the concave or compression side the walls remain thin, while the cells themselves become larger. In stems which were held in a horizontal position so that they could not bend upward under the stimulation of gravity, he observed the same results; the upper or stretched side had normal or slightly smaller cells with thickened walls, while the lower side had large thin-walled cells. NOW BORDNER'S results show that, under proper experimental conditions, tension causes a strengthening of stems by producing thicker walls; and it is shown that compression, when not too great, causes large thin-walled cells. It seems reasonable to say that tension and compression may be given as the two direct influences for the results observed by BÜCHER.

It is evident that the tension and compression do not have exactly opposite effects. We have seen that compression causes the cells to become larger and thus give greater surface for the osmotic pressure. Tension, as shown by the experiments of NOLL and HEGLER, tends to accelerate growth and cell division.

The two influences of tension and compression are thus both favorable to increase in the size of the organ subjected to them. Then if we accept the view of HEGLER and BORDNER, that tension may cause the walls to thicken, we have in an alternation of tension and compression all the necessary stimuli for increased size, growth, and strength in the part subjected to those stresses. It does not seem unreasonable to assume that intermittent or alternating compression and tension should have a greater stimulatory effect than a constant stress. It is very possible that under constant stress the internal equilibrium of stresses may come in time to be readjusted so that the external stress would be no longer felt. In experimental work this objection may be removed in part by increasing the stress from time to time. Yet it is easy to see that this could not have so much influence as the complete reversing of the stress from tension to compression and *vice versa*.

Summary

In the foregoing work the four woody stems show no increase in mechanical strength or in the amount or kind of mechanical tissue under the influence of longitudinal compression.

In young herbaceous stems the development of mechanical strength in the tissues is somewhat retarded by a longitudinal compression caused by comparatively heavy weights.

Neither light weights nor heavy weights have any appreciable effect upon the growth and strength of herbaceous stems which have already formed a cylinder of mechanical or woody tissue.

Continuous longitudinal compression causes no marked differences in the size or form of any part of the stem which is subjected to the compression, excepting of course mechanical changes which might be caused by excessive compression.

The investigation for which these results were obtained was carried out under the direction of Professor F. C. NEWCOMBE, to whom I wish to acknowledge my sincere thanks for his kindly interest and timely suggestions.

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THE NORTH AMERICAN SPECIES OF STEREOCAULON

LINCOLN WARE RIDDLE

(WITH NINE FIGURES)

The American species of *Stereocaulon* fall naturally into two groups. One is a typically boreal group, with *S. paschale* the central species, and a general distribution throughout British North America and the northern United States, as far south as North Carolina in the Alleghany Mountains, and in the Rocky Mountains extending into Colorado, and in the case of some of the species even into the mountains of Mexico and the South American Andes. The other group is a tropical one, represented by *S. ramulosum* and its allies, and characteristic of tropical America, from which it extends rather widely into the southern hemisphere. No American herbarium contains sufficient material for a satisfactory study of these tropical species, and for that reason the present paper is confined to a consideration of the boreal species.

Anyone who has attempted to determine material of *Stereocaulon*, or has studied the material in our herbaria, must have realized the confusion which exists in regard to the distinctive characters of the species. This confusion arises in part from the great variability of the species, and their tendency, in some cases, to intergrade. But another cause of the confusion comes from the lack of literature available to the general student and containing comparative notes on the species. This lack of comparative notes makes TUCKERMAN'S *Synopsis of the North American Lichens*, which has been the guide for most of the study of the American material, a difficult treatment to use. The classic work on the genus *Stereocaulon* is to be found in the papers of TH. M. FRIES, his *De Stereocaulis et Pilophoris commentatio* being published in 1857, and his *Monographia Stereocaulorum et Pilophororum* in 1858. These must form the basis for any careful study, but unfortunately they are rather inaccessible to American students.

The present paper is an attempt to clear up some of the existing

confusion and to provide an available account of the North American species of the boreal group, which shall include comparative notes, and shall cite the specimens to be found in some of our herbaria. I have been fortunate in having access, through the courtesy of Professor FARLOW, to the Tuckerman Herbarium, which contains authentic material of the following species:

S. coralloides Fr., S. denudatum Flke., S. nanodes Tuck., S. paschale var. conglomeratum Fr., S. tomentosum Fr., S. Wrightii Tuck., S. cereolinum Koerb., S. Despreaultii Del., S. glaucescens Tuck., and S. tenellum Tuck.

Professor FARLOW'S own herbarium contains an authentic specimen of *S. foliiforme* Hue; and Professor FINK has kindly communicated a specimen of *S. alpinum* Laur. from LAURER'S herbarium, which I have taken to be authentic.

In addition to the Tuckerman collection (cited as "Tuck"), the following herbaria have furnished the basis for study. The abbreviations in parentheses are those used in the body of this paper in the citation of specimens.

1. Cryptogamic Herbarium of Harvard University, including the personal collection of Professor W. G. FARLOW. (H)

2. Herbarium of Wellesley College. (W)

3. The CLARA E. CUMMINGS lichen collection, Wellesley College. (CEC)

4. The C. J. SPRAGUE collection at the Boston Society of Natural History. (BSNH)

5. Herbarium of the Thoreau Museum of Natural History, Middlesex School, Concord, Mass. (Th)

6. Herbarium of the University of Vermont, including the collections of C. C. FROST and Dr. C. G. PRINGLE. (UVM)

7. Herbarium of Brown University. (B)

8. Herbarium of Yale University. (Y)

9. Herbarium of the New York Botanical Gardens. (NY)

10. He barium of the Geological Survey of Canada. (Can)

11. The Mt. Desert Herbarium (in the possession of Mr. E. L. RAND). (Mt.D)

12. Herbarium of Professor BRUCE FINK, Oxford, Ohio. (F)

13. Herbarium of L. W. RIDDLE, Wellesley, Mass. (R)

If my interpretation of the principles of generic nomenclature

is correct, ACHARIUS should be cited as having definitely established the genus *Stereocaulon* in *Methodus Lichenum* (1803), p. 314, with *Lichen ramulosus* Swartz as the type species. It is true that the name had been used by three previous authors, but none of these can be held to have established the genus, according to present ideas. SCHREBER first published the name with a brief diagnosis in LINNAEUS' *Genera Plantarum*, ed. 8 (1791), p. 768, but no species is cited under the genus. SCHRADER, in *Spicilegium Florae Germanicae* (1794), p. 113, used the name with a single species, *S. corallinum*, a species based, however, on an imperfect lichen which later proved to be a *Pertusaria*. Finally, HOFFMAN, in *Deutschlands Flora*, II (1795), p. 128, gives a genus *Stereocaulon*, with nine species; of these nine only three are now recognized as belonging to the genus, the others included two species of *Sphaerophoron*, one *Collema*, one *Lichina*, and two imperfect forms; HOFFMAN'S genus, therefore, "embraced elements altogether incoherent" and hence cannot be considered valid. ACHARIUS thus remains the first author to place the genus on a solid foundation. The generic characters may be stated as follows:

Thallus of two parts, a primary horizontal thallus, which in most cases soon disappears, and erect, solid, cylindrical, ecorticate podetia; thallus of minute, rounded or irregularly flattened squamules, which are typically gray, sometimes creamy or white, and which also cover the podetia more or less thickly; apothecia lecideine; spores fusiform to acicular, hyaline, plurilocular. —Closely related to *Cladonia*, from which it differs in the solid podetia and the plurilocular spores, the latter character also serving to distinguish this genus from *Pilophorus*.

The term "squamules" (used by ACHARIUS, E. FRIES, SCHAERER, and others) is here adopted, in preference to the term "phyllocladia" (used by TH. FRIES and by TUCKERMAN), for the thalline outgrowths which constitute the thallus of species of the § PROSTEREOCAULON, and which occur so characteristically on the podetia of all species. The term is in current use for such thalline structures in other genera of lichens, and especially in the genus *Cladonia*, with which the squamules of *Stereocaulon* are strictly homologous, although somewhat modified.

In the descriptions of the species I have made no attempt to describe all the details of the plant, many of them unimportant,

but rather to give a diagnosis of the salient and characteristic features by which the species is to be recognized.

KEY TO THE SPECIES

This key is based on typical specimens. For the determination of intergrading forms, reference should be made to the comparative notes, which follow each species.

A. Plants chalky-powdery ..... 9. *S. albicans*

AA. Plants not chalky-powdery.

B. Primary thallus present.

C. Spores 4 μ wide, ends blunt; podetia frequently ending in soredia ..... 1. *S. pileatum*

CC. Spores 2.7 μ wide, ends pointed; podetia never ending in soredia ..... 2. *S. condensatum*

BB. Primary thallus absent.

C. True squamules absent, podetia ending in flattened, foliose tips ..... 8. *S. Wrightii*

CC. True squamules present.

D. Squamules of the palmate-digitate type (see fig. 7).

E. Podetia glabrous or faintly tomentose, cephalodia with *Stigonema*.

F. Podetia loosely branched and spreading 4. *S. paschale*

FF. Podetia in compact cushions 4*a*. *S. paschale* v. *conglomeratum*

EE. Podetia more or less densely tomentose, cephalodia with *Nostoc*.

F. Podetia repeatedly branched 5. *S. tomentosum*

FF. Podetia subsimple 5*a*. *S. tomentosum* v. *simplex*

DD. Squamules of some other type.

E. Squamules coralline ..... 3. *S. coralloides*

EE. Squamules umbilicate or coarsely granular.

F. Podetia glabrous, cephalodia with *Stigonema* 7. *S. denudatum*

FF. Podetia tomentose, cephalodia with *Nostoc* 6. *S. alpinum*

Section PROSTEREOCAULON

Primary thallus persistent and closely adnate to the substratum, podetia mostly short, under 2 cm., and simple or sparingly branched;

squamules poorly developed, mostly granular.—The species of this section show resemblance to *Pilophorus*.

KOERBER'S name "Cereolus" for this section must be abandoned, with the exclusion of the *Lichen cereolus* of ACHARIUS from the genus (see discussion under *S. pileatum*).

1. STEREOCAULON PILEATUM Ach.

S. pileatum Ach. Lich. Univ. p. 582. 1810.

S. condensatum Laurer in Fries Lich. Eu. p. 203, in part. 1831; and in Tuck. Syn. Lich. New Eng. p. 46, in part. 1848.

S. cereolus Schaerer Enum. Crit. Lich. Eu. p. 178. 1850; not Ach. Meth. p. 316. 1803.

S. cereolinum Koerber Syst. Lich. Germ. (1855) p. 14. 1855; not Ach. Syn. p. 285. 1814.

Primary thallus persistent, closely adnate to the substratum, formed of granular squamules which tend to become coralline; podetia short, mostly under 1 cm., and simple or nearly so, glabrous, with scattered coralline-granular squamules; apothecia terminal, or often absent and the podetia then ending in a mass of white soredia; spores 16.5–29×3.5–5 μ, average 21.4×3.9 μ, with blunt ends; cephalodia of the type of *S. paschale* (*q.v.*).—Growing on rocks.

SPECIMENS EXAMINED

EUROPE: Stenh. Lich. Suec. no. 85; Moug. and Nestl. no. 947; Koerb. Lich. sel. Germ. no. 271.

CANADA: Newfoundland, *Waghorne* 1893, as *S. nanodes* (Hb. Eckfeldt); Anticosti Is., *Macoun* Aug. 24, 1883 (Can); Cape Breton Is., *Macoun* July 22, 1898 (Can); Nova Scotia, *Macoun* 1883 (Tuck); *McKay* (BSNH); Grand Manan Is., *Willey* (BSNH).

MAINE: Mt. Desert, *J. W. Eckfeldt* 1888 (Mt. D); Rockland, *G. K. Merrill* (NY).

NEW HAMPSHIRE: White Mts., Tuckerman Lich. Exs. no. 113 in part; also *Tuckerman* in Herb.; Bald Mt., *W. G. Farlow* Sept. 1905 (H); Chocorua, *W. G. Farlow* Sept. 1907 (H); Fitzwilliam, *R. H. Howe, Jr.*, Aug. 6, 1909 (R).

VERMONT: Mt. Mansfield, *C. G. Pringle* no. 197 (BSNH); Willoughby, *G. G. Kennedy* July 28, 1898 (H).

MASSACHUSETTS: Chelmsford and Salem, *J. L. Russell* 1850 (Tuck); Concord, *R. H. Howe, Jr.* (Th); Ipswich, *Oakes* and *Tuckerman* Nov. 1842 (Tuck); New Bedford, *Willey* 1881 (Tuck).

NEW YORK: Adirondack Mts., *L. W. Riddle* Aug. 1908 (R).

This is the only species treated in this paper of which the synonymy is

confused, the uncertainty arising on account of the doubt as to what ACHARIUS meant by his *Lichen cereolus*, described in *Lichenographia Suecicae Prodromus* (1798), p. 89, and figured as *Stereocaulon cereolus* in *Methodus Lichenum* (1803), *pl. 7, fig. 1*. In TH. FRIES'S *Monograph* (1858), p. 40, the treatment is confused, *S. cereolus* being placed as a variety under *S. cereolinum* (Ach.) Koerb., of which *S. pileatum* is made a synonym, apparently disregarding priority. But in his *Lichenographia Scandinavica* (1871), p. 55, TH. FRIES states that according to the original specimens in ACHARIUS' Herbarium, *Lichen cereolus* is synonymous with *Pilophorus Fibula* Th. Fr. This would leave *S. pileatum* the oldest name and the one to be adopted, as has indeed been done by TH. FRIES (*op. cit.*) and most recent authors.

Stereocaulon pileatum is closely allied to *S. condensatum*, with which, as indicated in the synonymy, it was at one time united by certain authors, yet the differences between the two are greater than those between *S. paschale* and *S. tomentosum*, which have been recognized as distinct since the work of ELIAS FRIES. The points of difference are as follows.

S. pileatum	*S. condensatum*
1. Squamules typically coralline.	1. Squamules granular.
2. Podetia simple and reduced.	2. Podetia stouter, often branched above.
3. Apothecia often replaced by soredia.	3. Apothecia never replaced by soredia.
4. Spores with blunt ends, and averaging 4 μ in width.	4. Spores with pointed ends, and averaging 2.7 μ in width.
5. Growing on rocks.	5. Growing on soil.

S. pileatum also shows a strong resemblance to forms of *Pilophorus*. When fertile the spore differences will of course serve for their distinction.

2. STEREOCAULON CONDENSATUM Hoffm.

S. condensatum Hoffm. Deutsch. Fl. 2:130. 1795.

Primary thallus persistent, formed of coarse, rounded granules, intermixed with conspicuous black masses of *Stigonema*, with which are formed dark, rugose cephalodia; podetia stout, simple or fastigiately branched above; squamules granular, rarely coralline; apothecia well developed; spores 20–28×2.5–3 μ, average 23×2.6 μ, with pointed ends.—Growing on soil.

SPECIMENS EXAMINED

EUROPE: Fries Lich. Suec. no. 88; Schaer. Lich. Helv. no. 509; Anzi Lich. Ital. Suppl. no. 29; Nyl. and Norrl. Herb. Lich. Fenn. no. 87.

CANADA: Labrador, *A. P. Low* July 21, 1896 (Can); Quebec, *Macoun* Aug. 11, 1905 (Can).

MASSACHUSETTS: Wellesley, *Clara E. Cummings* in Dec. N. A. L. 26; South Sudbury, *C. M. Carr* (R); Ipswich, *Wm. Oakes* (Tuck); Duxbury, *J. L. Russell* (Tuck); New Bedford, *H. Willey* (BSNH); Mattapoisett, H. *Willey* (R).

CONNECTICUT: Montville, *W. A. Setchell* (Tuck); Norwich, *W. A. Setchell* (H).

The differences which distinguish this species from *S. pileatum* are sufficiently indicated in the notes under the latter, to which reference may be made.

Section EUSTEREOCAULON

Primary thallus soon disappearing; podetia mostly tall, well developed, and irregularly branched; squamules well developed, cartilaginous, gray or white, but never chalky.—Spores 15–35× 2.5–5 μ, with some minor variations among the species, but on the whole so uniform as to be without value in specific diagnosis.

3. STEREOCAULON CORALLOIDES Fries.

S. coralloides Fries Lich. Suec. no. 118. 1817; and Sched. Crit. p. 24. 1824.
S. corallinum Laurer in Fries Lich. Eu. p. 201. 1831.
S. corallinum Fries in Tuck. Syn. Lich. N.E. p. 45. 1848.
S. Despreaultii Delise ms. in Nyl. Syn. p. 249. 1858 (according to authentic specimen in Herb. Tuck.).

Podetia solitary or caespitose, erect, branched, usually extensively, glabrous or subtomentose; squamules coralline and branching, giving the plant a fibrillose appearance; apothecium medium to large (1–4 mm.), mostly terminal; cephalodia of the type of *S. paschale* (*q.v.*), usually abundant and conspicuous.—Growing on rocks (fig. 5).

SPECIMENS EXAMINED

EUROPE: Fries Lich. Suec. no. 118; Stenh. Lich. Suec. no. 82; Sweden, *Th. Fries*, Leighton Collection (NY), also *Nylander* (*loc. cit.*); Schaer. Lich. Helv. no. 261; Hepp Lich. Eu. no. 114; Pyrenees, *R. Spruce* in Leighton Collection (NY).

BRITISH AMERICA: Labrador, *Townsend* July 1906 (H); Newfoundland, *Waghorne* no. 46, no. 66 as *S. tomentosum*, no. 67 as *S. paschale* (CEC); New Brunswick, *Farlow* July 1892 (H); *Willey* (Tuck); Cape Breton Is., *Macoun* July 22, 1898 (Can); Nova Scotia, *A. H. Mackay* (BSNH); Ontario, *Macoun* (Can); Lake Superior, *Macoun* (Can); Vancouver Is., *Macoun* (Can); *Calder* (BSNH); *Lyall* (Tuck).

ALASKA: Unalaska, *J. M. Macoun* June 4, 1897 (Can); St. Paul Is., *J. M. Macoun* June 19, 1897 (Can).

MAINE: Eastport, *Farlow* (H); West Pembroke, *Maude C. Wiegand* Aug. 11, 1909 (W); Mt. Katahdin, *J. F. Collins* in Herb.; Mt. Desert Is., *M. L. Wilson* (Mt. D).

NEW HAMPSHIRE: White Mts., Tuckerman Lich. Exs. no. 94; *E. Faxon*, as *S. denudatum* (CEC); *Clara E. Cummings* (R); *Farlow* (H).

VERMONT: Brattleboro, *C. C. Frost* (UVM).

NORTH CAROLINA: *Buckley* (NY); *J. W. Harshberger* (NY).

A beautiful species, entirely distinct from all others of the boreal group in the coralline or fibrillose squamules (fig. 8), clearly separating it from *S. paschale* and *S. tomentosum*, which it resembles in habit. Although much the rarest of the three species, it is nevertheless rather remarkable that no specimens have been seen from the central or western parts of the United States.

4. STEREOCAULON PASCHALE (L.) Ach.

Lichen paschalis Linnaeus Sp. Pl. **2**:1153. 1753 (cf. WAINIO *Revisio lichenum in herbario Linneai asservatorum* in Medd. Soc. F. et Fl. Fenn. **14**:1. 1886).

Stereocaulon paschale Acharius Meth. Lich. p. 315. 1803, in part (cf. TH. FRIES Monog. Ster. p. 58).

Stereocaulon paschale Fries emend. in Lich. Eu. p. 202. 1831.

Podetia 3 to 9 cm. high (average 6 cm.), caespitose, lax, spreading, procumbent, or rarely erect, more or less intricately branched throughout, glabrous or somewhat tomentose; squamules palmate-digitate, or margin crenate, or, on upper part of podetia, granulate, never coralline; apothecia 0.5 to 4 mm. in diameter, average 1 mm., terminal or terminal and lateral; cephalodia typically conspicuous, gray, spherical, rugose-plicate, containing *Stigonema*, sometimes fibrillose and black.—Growing on rocks, rarely on the earth.

SPECIMENS EXAMINED

EUROPE: Stenh. Lich. Suec. no. 80; Sweden, *Th. Fries* 1854, and *Tuckerman* 1842 (Tuck).

BRITISH AMERICA: Labrador, *A. P. Low* July 1896 (Can); *Waghorne*, Aug. 1891 (NY); Quebec, Gaspe County, *J. F. Collins* July 19, 1906 (R); New Brunswick, *G. U. Hay* July 1884 (Can); Nova Scotia, *Mackay* (BSNH); Ontario, many localities, *Macoun* (Can); Lake Superior, *Macoun* Canad. Lich. no. 45; Alberta, *H. L. Bolley* Aug. 1901 (F); British Columbia, *Macoun* (Can).

ALASKA: *J. M. Macoun* 1892 (Can); Sheep Creek near Juneau, *Grace E. Cooley* Aug. 5, 1891, as *S. tomentosum* (CEC); Muir Glacier, *Trelease* June 9. 1899, Harriman Exped. no. 1299, as *S. tomentosum* (CEC); Port Cla en ,

Behring Strait, *Trelease* July 12, 1899, Harriman Exped. no. 1266, as *S. tomentosum* (CEC).

MAINE: Eastport, *W. G. Farlow* 1877 (Tuck); Portage, *L. W. Riddle* Aug. 1907 (R); Rangeley *L. W. Riddle* Aug. 1904 (R); Orono, *L. W. Riddle* July 1907 (R); Mt. Desert, *M. L. Wilson* (Mt. D), *Sam Surrey* (R); Rockport, *G. K. Merrill* Lich. Exs. no. 40; Cumberland, *J. Blake* (NY).

NEW HAMPSHIRE: White Mts., Tuckerman Lich. Exs. no. 122; North Woodstock, *Clara E. Cummings* in N. A. L. no. 25, L. B. A. no. 151; Crawfords, *Miss Minns* (W); Warren, *Charles W. Riddle* Aug. 1908 (R); Mt. Chocorua, *H. H. Bartlett* Sept. 1906 (R); Mt. Monadnock, *W. G. Farlow* (H); *R. H. Howe, Jr.* (Th); Fitzwilliam, *R. H. Howe, Jr.*, Lich. Nov. Ang. no. 22.

VERMONT: Mt. Mansfield, *C. G. Pringle* 1879 (UVM); Willoughby, *W. G. Farlow* (H); Bristol, *L. W. Riddle* Aug. 12, 1908 (R).

MASSACHUSETTS: Pepperell, *L. W. Riddle* May 30, 1909 (R); Mt. Watatic and Concord, *R. H. Howe, Jr.* (Th); Arlington, *B. Fink* May 1895 (R); "near Boston," *T. P. Adams* (BSNH).

CONNECTICUT: Woodbridge, *G. E. Nichols* March 13, 1909 (R).

NEW YORK: Adirondack Mts., *Mrs. C. W. Harris* 1900 (R); *L. W. Riddle* Aug. 1908 (R).

OHIO: *Lesquereux?* (NY).

MICHIGAN: *E. T. Harper* Aug. 1899 (R).

WISCONSIN: *C. F. Baker* (CEC).

MINNESOTA: *Macmillan* 1894 (R); *B. Fink* July 30, 1902 (R).

OREGON: *E. Hall* 1871 (Tuck).

TUCKERMAN, following TH. FRIES, cites E. FRIES as the author of this species. The combination was first made, however, by ACHARIUS (*op. cit.*), who refers to the figure in *English botany, pl. 282*. According to the Vienna Code (Articles 40 and 41), ACHARIUS should be cited therefore as the author, even though his conception of the species was later emended by FRIES through the segregation of *S. tomentosum* and *S. coralloides*.

S. paschale is the commonest and most widely distributed species of the genus, at least in the eastern portion of North America. In the west it seems to be comparatively rare, its place being taken by *S. tomentosum*.

The two species named may be best separated from their allies by the palmate-digitate type of squamules (fig. 7). The chief difficulty, however, comes in finding satisfactory characters to distinguish *S. paschale* from *S. tomentosum*. Typical *S. paschale* is said to have glabrous podetia, while in *S. tomentosum* they are said to be densely tomentose. But a study of a sufficient amount of material shows that there are all gradations from wholly glabrous podetia through a medium amount of tomentum to densely tomentose. As the tomentum is the chief character hitherto used as diagnostic, it is clear that with such variability much confusion must result. A second character which has been used is the position of the apothecia, in typical *S. paschale*

the apothecia being at least in part terminal, while in *S. tomentosum* they are said to be always lateral. Here again we have a variable character which cannot be used as a precise criterion.

In searching for a character which would by its nature be mutually exclusive for the two species, the attempt was made to use the cephalodia. The differences between the cephalodia typical of these two species are sufficiently indicated in the descriptions, to which reference may be made. To establish the taxonomic value of this structure, it was necessary to prove three points: first, both types of cephalodia must not occur on the same plant; secondly, the cephalodia must be constant enough in occurrence to be of use; and thirdly, the characteristics of the cephalodia must be correlated with the other diagnostic characters.

As has been shown by various investigators, the cephalodia of lichens are peculiar gall-like outgrowths formed by the hyphae of the thallus surrounding some foreign alga. A priori we should hardly expect that such a structure would be constant enough to be used in classification. The method adopted to prove the points mentioned was to make a statistical study of a large number of specimens of the *paschale-tomentosum* group, noting the type of cephalodium, the amount of tomentum, and the position of the apothecia, and then to tabulate the results. In this statistical study material was examined from various parts of North America and Europe, and the specimens were taken as they came in the herbaria, in order to avoid influencing the results by conscious choice. The only exception was made in the case of a few specimens which were so clearly depauperate that they could in no way be looked upon as aiding in the object sought. The results are given in the following tables:

Number of specimens examined	103
Specimens with both types of cephalodia	1
Specimens lacking cephalodia	9
Specimens lacking apothecia	22

The fact that on only one specimen studied were both types of cephalodia found shows that for practical purposes the two types are mutually exclusive. Cephalodia being present in a larger proportion of specimens than were apothecia, it follows that if apothecial characters or spore characters are of value cephalodia can equally well be used, as far as constancy of occurrence is concerned. To show correlation of characters, the results may be arranged as follows:

Cephalodia	Apothecia		
	Terminal	Mixed	Lateral
Tomentosum type	1	13	28
Paschale type	11	18	3

Cephalodia	Tomentum		
	Absent	Medium	Abundant
Tomentosum type....	0	16	34
Paschale type.....	24	19	0

These tables show conclusively the extent to which *S. paschale* and *S. tomentosum* intergrade. They show also the confusion introduced by taking the presence of tomentum alone as a criterion, for, as is shown in the second table, out of 93 specimens 35 were intermediate in the amount of tomentum. With such intergrading, complete correlation of characters is not to be expected. But the tables show that the types of cephalodia are correlated to a marked degree with the two characters that have been recognized as of chief importance in separating these two species. The results of the statistical study, therefore, support very strongly the suggestion that the cephalodia, when present, are of great taxonomic value. Yet taking all available characters into consideration, there are still specimens which cannot be placed absolutely under either of these species, but exhibit characters of both. And this must necessarily be so on account of the fact that in nature *S. paschale* and *S. tomentosum* evidently form a continuous, variable series, the forms that we recognize as "typical" being merely the two extremes of this series.

Of the numerous forms of *S. paschale* which have been distinguished by European authors only one seems to be of sufficient importance in North America to receive separate treatment. This is

4*a*. Stereocaulon paschale var. conglomeratum Fries.

Fries Sched. Crit. ad Lich. Suec. 3:20. 1824.

Podetia much branched, forming compact cushions which are closely adnate to the substratum, squamules more granular and crowded than in the type; usually sterile.—Growing on rocks.

SPECIMENS EXAMINED

Europe: Fries Lich. Suec. no. 89; Hepp Lich. Eu. no. 304; Sweden, *Areschoug* (Tuck).

New Hampshire: Mt. Monadnock, *W. G. Farlow* July 1, 1896 (H); Alton Bay, *C. J. Sprague* (BSNH).

Vermont: Mt. Ascutney, *R. H. Howe, Jr.*, Aug. 25, 1909 (Th).

Massachusetts: Annisquam, *Clara E. Cummings* 1892 (CEC); Wellesley, *Clara E. Cummings* Dec. 1884 (CEC); *L. W. Riddle* Jan. 1908 (R).

This is a reduced form of *S. paschale*, occurring either at low altitudes or on rocks with extreme exposure. It passes into the laxer, more typical form by insensible gradations. The only other species with which this variety may

be confused is *S. denudatum*, and the specimens from Ipswich, Mass. (*Wm. Oakes*), and from Nantasket, Mass. (*H. Willey*), in the Tuckerman Herbarium, labeled *denudatum*, seem to be much nearer this variety of *S. paschale*. The two have a general resemblance in habit, but *S. paschale* var. *conglomeratum* is less denuded and always has indications of the palmate-digitate type of squamules typical of *S. paschale*.

5. STEREOCAULON TOMENTOSUM Fries.

S. tomentosum Fries Sched. Crit. ad Lich. Suec. 3: 20. 1824.

FIGS. 1, 2, 3.—Fig. 1, *Stereocaulon tomentosum* Fr., typical form; specimen from Disenchantment Bay, Alaska, collected by W. TRELEASE, June 19, 1899, Harriman Exped. no. 1297, in herbarium of CLARA E. CUMMINGS; photo. nat. size; fig. 2, *Stereocaulon tomentosum* Fr., large form; specimen from Cascade Mts., Oregon, collected by C. G. PRINGLE, Sept. 20, 1881, in herbarium of Wellesley College; photo. nat. size; fig. 3, *Stereocaulon Wrightii* Tuck.; specimen from St. Michael, Alaska, collected by W. A. SETCHELL, University of California Expedition, 1899, in herbarium of CLARA E. CUMMINGS; photo. nat. size.

Podetia loosely attached to the substratum, erect, or spreading, 3 to 9 cm. high, average 5 cm., more or less densely tomentose; squamules palmate-digitate, abundant, more or less crowded; apothecia typically minute, 0.5 to 1 mm. in diameter, rarely larger, reaching 2 mm., lateral; cephalodia minute, verdigris-green, containing *Nostoc*.—Growing on the ground or among mosses, rarely on rocks (fig. 1).

SPECIMENS EXAMINED

EUROPE: Fries Lich. Suec. no. 90; Stenh. Lich. Suec. no. 79; Hepp Lich. Eu. no. 302; Rabenh. Lich. Eu. no. 133; Lojka Lich. Hungarici no. dh; Upsala, *Th. Fries* 1854 (Tuck); Sweden, *Nylander* in Leighton Coll. (NY).

BRITISH AMERICA: Labrador, *Waghorne* no. 33, as *S. denudatum* (CEC); Anticosti, *Macoun* Aug. 22, 1883 (Can); New Brunswick, *G. U. Hay* June 24, 1882 (Can); Gaspe County, Quebec, *Macoun* July 28, 1882 (Can); *J. F. Collins* Aug. 17, 1906 (R); Cape Breton Is., *Macoun* July 9, 1898 (Can); Nova Scotia, *Macoun* June 12, 1883 (Can); Great Bear Lake, *Richardson* (H); Lake Superior, *Macoun* July 29, 1869 (Can); *Agassiz* 1848 (Tuck); British Columbia, many localities, *Macoun* (Can); *G. Dawson* Oct. 5, 1888 (Can); Alberta, *Macoun* June 13, 1907 (Can); *L. R. Waldron* June 16, 1901 (F).

ALASKA: *Dr. Kellogg* (Tuck); *P. M. Newhall* on Univ. Calif. Exped. 1899 (CEC); *Trelease* in Harriman Exped. nos. 1267, 1297, 1300, 1301; *Coville* and *Kearney* in Harriman Exped. nos. 609, 981, 2121 (CEC).

MAINE: Eastport, *Farlow* (H); Mt. Desert, *M. L. Fernald* Sept. 18, 1892 (CEC); Cumberland, *J. Blake* Dec. 1855 (CEC).

NEW HAMPSHIRE: White Mts., Tuckerman Lich. Exs. no. 23; Crawfords, *Miss Minns* (W); North Woodstock, *Clara E. Cummings* Aug. 19, 1892 (CEC); Shelburne, *Farlow* Aug. 1894 (H); Fitzwilliam, *R. H. Howe, Jr.* (Th.)

VERMONT: Hinesburgh, *C. G. Pringle* 1878 (UVM); Brattleboro, *C. C. Frost* (UVM).

MASSACHUSETTS: Magnolia, *C. J. Sprague*, as *S. paschale* (BSNH); Duxbury, *J. L. Russell* (B); New Bedford, *H. Willey* (B).

CONNECTICUT: Ellsworth, *H. A. Green* Aug. 7, 1887 (NY).

NEW YORK: *C. F. Austin* (NY); *E. A. Burt* (F); *K. M. Wiegand* (W); *L. W. Riddle* (R).

ILLINOIS: *J. Wolf* 1888 (NY).

MINNESOTA: Various localities, *B. Fink*, in Herb.; *Macmillan* (F).

COLORADO: *T. S. Brandegee* (R); *F. E. Clements*, as *S. paschale* (H).

MONTANA: *T. A. Williams* in Dec. N. A. L. no. 292.

WYOMING: *Aven Nelson* no. 2690 (NY).

WASHINGTON: *W. W. Calkins* no. 340, as *S. paschale* (W); Puget Sound *B. Fink* June 30, 1906 (F); Longmire's Springs, *E. T. Harper* Aug. 1906 (F).

OREGON: *C. G. Pringle* Sept. 20, 1881 (W); *E. Hall* 1871 (H); *J. W. Eckfeldt* 1882 (Can).

The relationship of *S. tomentosum* to *S. paschale* is sufficiently discussed under the latter species, to which reference may be made. The palmate-digitate type of squamules will serve to distinguish these species from others having the same habit, including *S. alpinum*, our only other species with typically tomentose podetia.

Certain material has been examined from our northwest coast, especially from the Cascade Mts., Oregon, which seemed at first to be distinct from *S. tomentosum* (fig. 2). These specimens are unusually large and finely developed, with large apothecia, and bearing conspicuous white structures which at first appeared to be a new type of cephalodium. Examination of these structures failed to show any type of alga other than the *Cystococcus*, which forms the normal gonidia for the genus, and the structures cannot therefore be considered cephalodia. After careful study I am unable to look upon this Oregon material as anything more than exceptionally luxuriant *S. tomentosum*.

It is otherwise, however, with another form of *S. tomentosum*, which is undoubtedly of varietal rank and may be designated

5*a*. STEREOCAULON TOMENTOSUM var. **simplex,** var. nov.

Podetia 6–9 cm. alta, erecta, simplicia vel subsimplicia; squamulae paucae et dispersae; tomentum et apothecia et cephalodia ut in forma typica.—Habitat in locis arenosis.

Podetia 6–9 cm., tall, erect, simple or nearly so; squamules few and scattered; tomentum, apothecia, and cephalodia as in the type.—Growing in bare sandy soil (fig. 4).

Type specimens: "On sandy river bottom, Mt. Rainier region, Washington," collected by *T. C. Frye*, Aug. 14, 1904, in Herb. L. W. Riddle.

Co-type specimens: in Herb. Fink and Herb. Wellesley College.

SPECIMENS EXAMINED

OREGON: Cascade Mts., *Moses Craig* Aug. 1898 (CEC), *A. S. Foster* June 20, 1907 (R).

WASHINGTON: Mt. Rainier region *T. C. Frye* Aug. 15, 1904 (R); Olympic Mts., *T. C. Frye* Aug. 7, 1907 (R).

BRITISH COLUMBIA: Salt Spring Is. Gulf of Georgia, *Macoun* May 9, 1887 (Can).

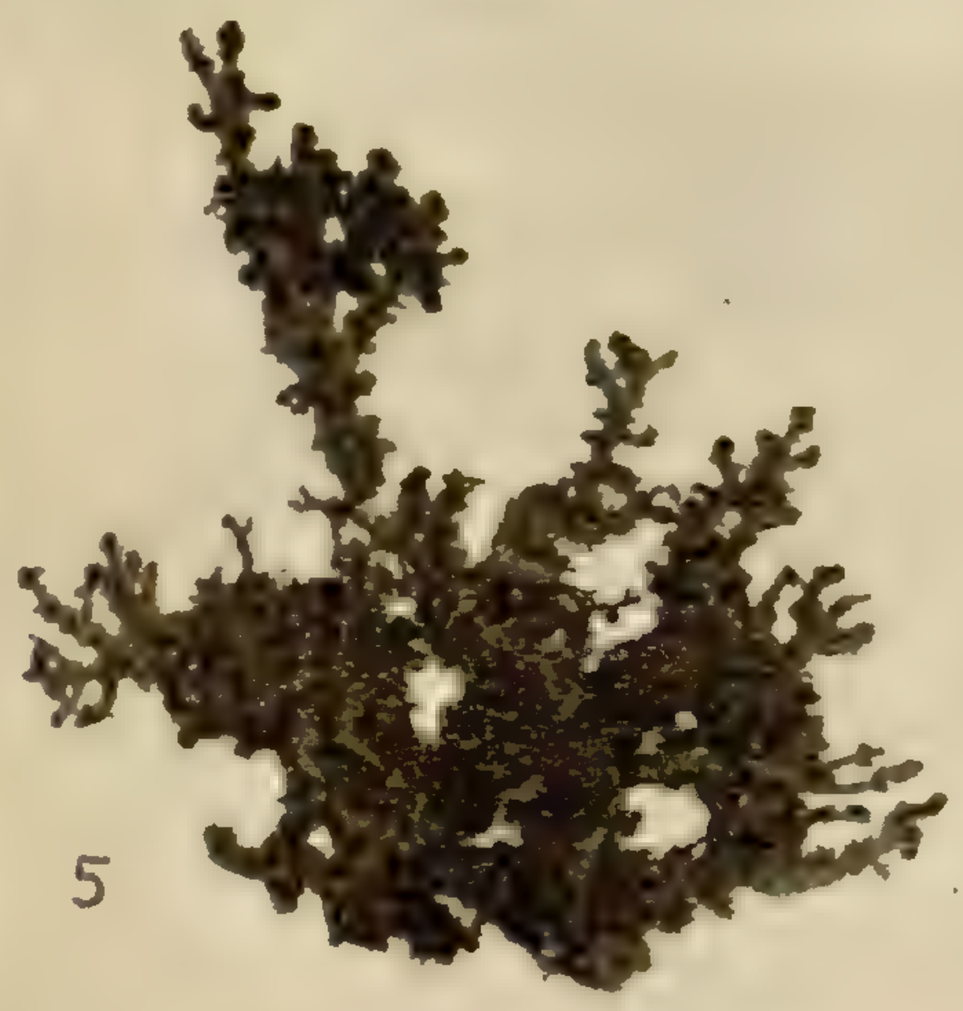
ALASKA: Davidson Glacier, *Grace E. Cooley* Aug. 15, 1891 (CEC).

This variety is very striking and distinct, and can scarcely be confused with any other North American form.

6. STEREOCAULON ALPINUM Laurer.

S. alpinum Laurer in Fries Lich. Eu. p. 204. 1831.

S. tomentosum var. *alpinum* (Laur.) Th. Fr. Comm. Ster. p. 30. 1857, and American authors.



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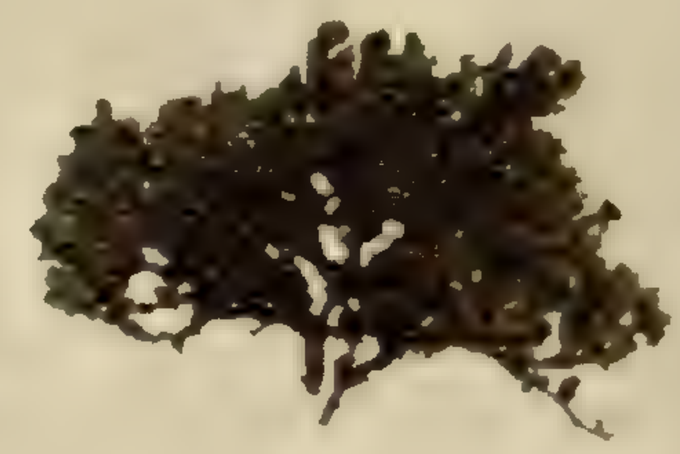

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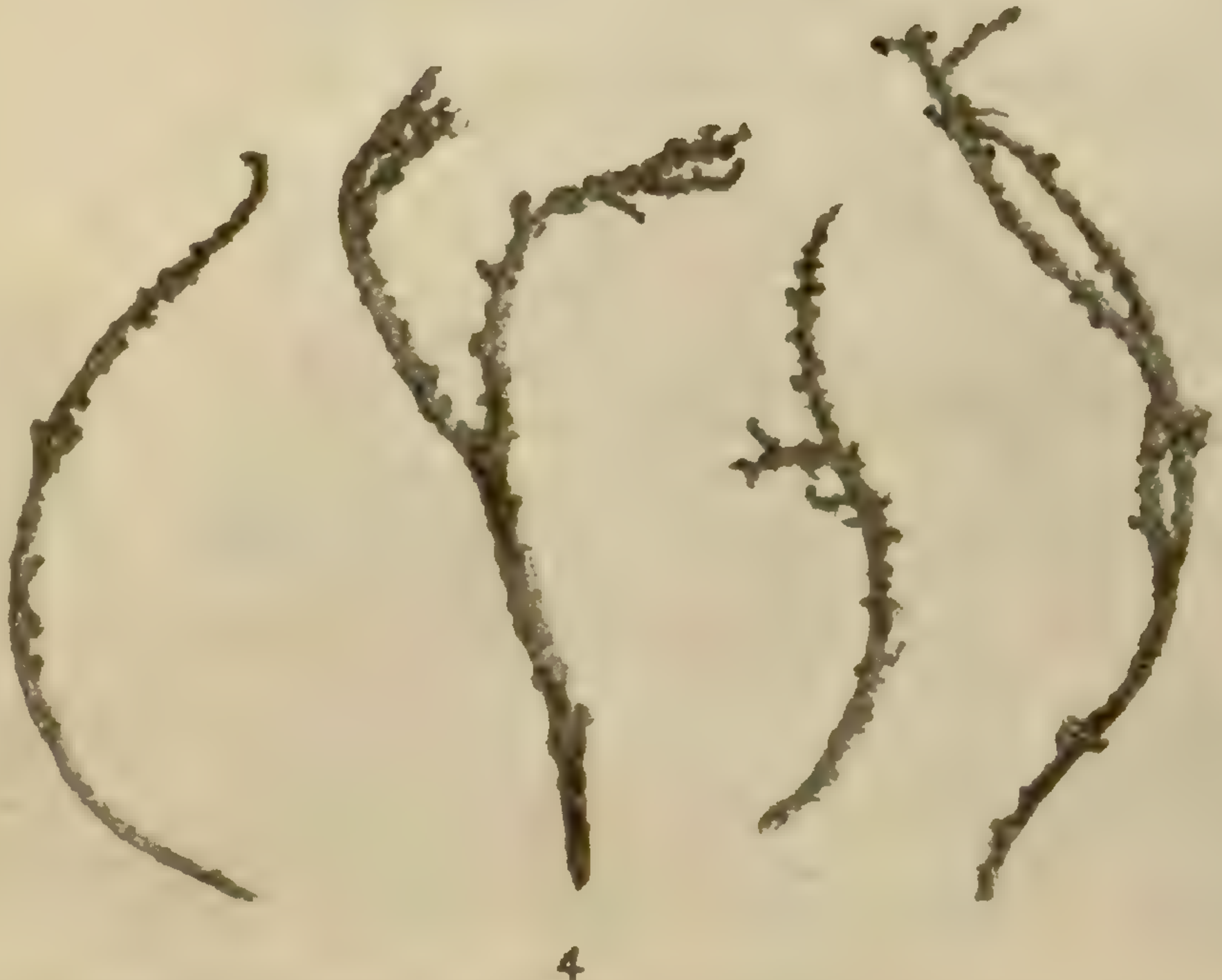

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FIGS. 4, 5, 6.—Fig. 4, *Stereocaulon tomentosum* var. *simplex* Riddle; type specimens from Mt. Rainier region, Washington, collected by T. C. FRYE, Aug. 14, 1904, in herbarium of L. W. RIDDLE; photo. nat. size; fig. 5, *Stereocaulon coralloides* Fr.; specimen from the Austrian Tyrol, collected by KERNSTOCK and issued in *Kryptogammae Exsiccati* (Vienna), no. 355, herbarium of L. W. RIDDLE; photo. nat. size; fig. 6, *Stereocaulon denudatum* Floerke; specimen with the granulate type of squamules, from Minnesota, collected by BRUCE FINK, June 19, 1897, in herbarium of L. W. RIDDLE; photo. nat. size.

Podetia stout, erect, 1 to 6 cm. tall, more or less densely branched, and tomentose; squamules in the form of coarse, crowded, conglomerate granules; apothecia (rare) medium to large, lateral or terminal; cephalodia of the type of *S. tomentosum* (*q.v.*).—Growing on exposed soil, especially in arctic-alpine regions.

SPECIMENS EXAMINED

EUROPE: Authentic specimens ex Herb. Laurer (F); Schaer. Lich. Helv. no. 263; Massalongo Lich. Ital. no. 11; Anzi Lich. Ital. Suppl. no. 26; Rabenh. Lich. Eu. no. 859; Arnold Lich. Exs. 5 no. 641*a;* Finmark, *Th. Fries* (Tuck).

BRITISH AMERICA: Greenland, *Fink* (NY); Cumberland Is., *Howgate Exped.* 1877 (Tuck); Diggs Is. Husdon Bay, *R. Bell* (Can); Labrador, *Waghorne* no. 20, also no. 21 as *S. condensatum* (CEC); *A. P. Low* (Can); Alberta, *Macoun* June 28, 1905 (Can).

ALASKA: St. Paul Is., *T. C. Kincaid* (F); Is. in Behring Strait, *C. Wright* (Tuck); Port Foulke, *Dr. Hayes* (Tuck); *Fred Funston* 1894 (CEC); *Trelease* in Harriman Exped. nos. 1268, 1270, 1298*a* (CEC); *Dall* in Harriman Exped. no. 1295, as *S. tomentosum* (CEC).

MAINE: Eastport, *Farlow* (H); Portage *L. W. Riddle* Aug. 1907 (R).

NEW HAMPSHIRE: Mt. Washington, *Farlow* Sept. 1894 (H).

MINNESOTA: *B. Fink* no. 93 (F).

OREGON: Mt. Hood, *E. Hall* 1871 (Tuck).

WASHINGTON: Mt. Rainier, *C. V. Piper* 1895 (CEC); Friday Harbor, *B. Fink* June 28, 1906 (F).

This is clearly distinct as a species from *S. tomentosum*, as the type of squamules is a specific criterion throughout the genus. It is most liable to confusion with *S. denudatum* which it resembles in general habit and range, but it can be distinguished by the tomentum and the type of cephalodium.

7. STREOCAULON DENUDATUM Floerke.

S. denudatum Flke. Deutsch. Lich. **4**:13. 1819.

S. glaubescens Tuck. Bost. Journ. Nat. Hist. **3**:302. 1840 (according to original specimen).

Podetia 2 to 4 cm. high, solitary or aggregated, shrubby-erect, subsimple below, branching above, wholly glabrous, denuded below, squamulose above; squamules crowded, in the typical form umbilicate, attached by the center, and with the margin crenate (see fig. 9), or often in the form of coarse, rounded, conglomerate granules; apothecia rare in North American specimens; cephalodia of the type of *S. paschale* (*q.v.*).—Growing on exposed rocks or soil (fig. 8).

SPECIMENS EXAMINED

EUROPE: Authentic specimen ex Herb. Floerke in Herb. Tuck.; Fries Lich. Suec. no. 346; Arnold Lich. Exs. no. 1576; Sweden, *Forssell* 1880 (NY); Scotland, *Leighton* July 1869 (NY); France, *L. Breviere* (R).

BRITISH AMERICA: Greenland, *Eberlin* 1885 (Can); *Warming* and *Holm* 1884 (H); Kikkeston Is., *Howgate Exped.* 1877 (Tuck); Hudson's Strait, *R. Bell* 1884 (Can); Labrador, *Wm. Palmer* 1887 (NY); *Owen Bryant* Aug. 22, 1908 (H); Newfoundland, no collector given (BSNH); *Delise* (Tuck) not typical.

NEW HAMPSHIRE: White Mts., Tuckerman Lich. Exs. no. 114; Mt. Washington, *W. G. Farlow* Sept. 1891 (H); Mt. Adams, *W. G. Farlow* Sept. 1897 (H); Mt. Willard, *E. Faxon* June 1882 (CEC); Mt. Monadnock, *W. G. Farlow* July 1896 (H).

VERMONT: *C. C. Frost* (BSNH); Mt. Mansfield, *W. G. Farlow* Sept. 1890 (H).

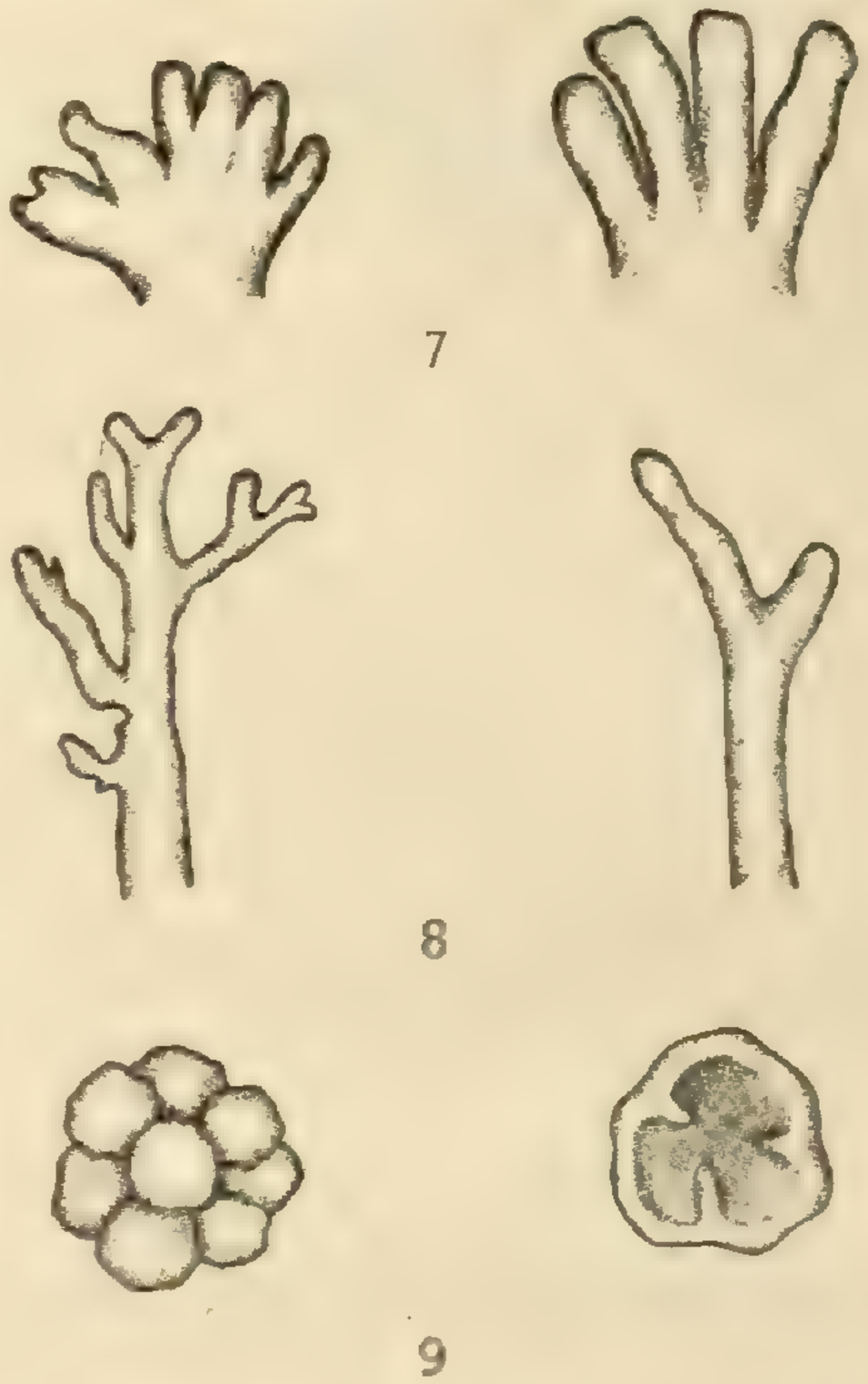
NEW YORK: *Mrs. C. W. Harris* June 1900 (R); Adirondack Mts., *W. G. Farlow* Sept. 1902 (H).

MASSACHUSETTS: Mt. Holyoke, *Whitman* May 20, 1839 (Tuck).

MINNESOTA: *B. Fink* no. 49 in Herb.

WASHINGTON: *Suksdorf* (BSNH).

CALIFORNIA: *Bolander* in Herb. Tuck. (doubtful!).



FIGS. 7, 8, 9.—Fig. 7, palmate-digitate type of squamules found in *S. paschale* and *S. tomentosum;* enlarged; fig. 8, typical squamules of *S. coralloides;* enlarged; fig. 9, squamules of *S. denudatum;* right, umbilicate type; left, granular type; enlarged and semi-diagrammatic.

ALASKA: *Dr. Kellogg* 1867 (Tuck); *W. A. Setchell,* Univ. Calif. Exped. 1899 (CEC); *W. H. Evans* 1897, as *S. alpinum* (CEC); *Harriman Exped.* no. 1279, as *S. alpinum* (CEC).

The two types of squamules described for this species intergrade, and the granulate type is scarcely worthy of varietal rank. The typical umbilicate squamules are found in specimens from arctic or subarctic stations. When these are present there should be no difficulty in distinguishing *S. denudatum* from all other species. But specimens with the coarsely granular squamules are less distinctive, and are frequently mistaken for either *S. paschale* or *S. alpinum.* From the latter the wholly glabrous podetia and the type of cephalodia should serve to distinguish *S. denudatum;* while the error of mistaking it for *S. paschale* may be avoided if it is borne in mind that in true *S. paschale*

some indication of the characteristic palmate-digitate type of squamules is always to be seen, and this type is never to be found in *S. denudatum*.

The most puzzling specimens that I have seen are those collected in New Jersey by C. F. AUSTIN. Portions of this material have been examined in the Tuckerman Herbarium, the Sprague Collection at the Boston Society of Natural History, and the Herbarium of the New York Botanical Gardens. It was determined by TUCKERMAN as *S. denudatum*, and is cited in his *Synopsis of North American Lichens*, p. 233; yet it is scarcely typical of this species, and it seems much nearer to *S. paschale*, a view which would be supported by the latitude of the station, *S. denudatum* being essentially an arctic-alpine species.

According to the description of this species given by TH. FRIES, the apothecia are minute (i.e. about 0.5 mm. in diameter) and lateral. But the specimen collected by C. C. FROST in Vermont and now in the Sprague Collection (BSNH), agreeing in all other particulars with *S. denudatum*, has terminal apothecia, over 1.5 mm. in diameter.

8. STEREOCAULON WRIGHTII Tuck.

S. Wrightii Tuck. Suppl. II to Enum. N. Am. Lich. in Am. Journ. Sci. **28**:202. 1859.

Stereocladium Wrightii Nyl. Lich. Freti Behr. p. 85. 1888.

Stereocaulon foliiforme Hue Bull. Soc. Bot. France **54**:414. 1907 (see below).

Podetia 1 to 4 cm. tall, solitary or caespitose, branched above, wholly glabrous, denuded below, ending in broad, foliose, convolute tips, taking the place of the usual squamules; or the podetia reduced and the expanded portions alone present; apothecia unknown; cephalodia doubtful (fig. 3).

Hitherto this species has been known only from the type collection made by CHARLES WRIGHT at Arakamtchetchene Is. on the Asiatic side of Behring Strait, during the U.S. North Pacific Exploring Expedition (1853–1856). To this may now be added two other localities, from both of which specimens have been distributed under other names. A comparison of these specimens, however, with the type specimens of *S. Wrightii* in the Tuckerman Herbarium shows that they are undoubtedly this species. These specimens are from St. Michael, Alaska, collected by W. A. SETCHELL on the University of California Expedition in 1899, and distributed as *Stereocaulon denudatum;* and from Shiribeshi, Japan, collected by ABBE FAURIE, July 1905, and issued in Faurie Lich. Jap. no. 6999 as *Stereocaulon foliiforme* Hue, n. sp.; an authentic specimen determined by HUE himself is in the herbarium of W. G. FARLOW.

Section CHONDROCAULON (*Leprocaulon* Nyl.)

Primary thallus present or disappearing; podetia reduced, simple or branched; squamules granular, dissolving into chalky-white powder.

9. STEREOCAULON ALBICANS Th. Fr.

S. albicans Th. Fr. Comm. Ster. p. 36. 1857.

S. tenellum Tuck. Bot. Wilkes Voy. p. 123. 1861 (according to type specimens).

Podetia short, mostly under 1 cm., slender, caespitose, branched, crowded and intertangled; squamules minutely granular, becoming powdery; apothecia unknown.—The whole plant is characteristically chalky-white and powdery.

SPECIMENS EXAMINED

NORTH AMERICA: Greenland, Kikkeston Is., *Howgate Exped.* 1877 (Tuck); Vancouver Is., *Macoun* May 19, 1893 (Can); Colorado, *T. S. Brandegee* (BSNH); Arizona, Rincon Mts. near Tucson, *J. C. Blumer* Oct. 1909 (R); California, *C. R. Orcutt* (BSNH); *W. G. Farlow* (H); Guadeloupe Is., *E. Palmer* 1875 (Tuck); Cuba, *C. Wright* (Tuck).

SOUTH AMERICA: New Granada, *Lindig* no. 2502 (Tuck); Peru, *Wilkes Exped.* (Tuck), type of *S. tenellum* Tuck.

This is a rare and interesting species, first described by TH. FRIES from material collected by GAUDICHAUD in Peru, but with a wide distribution as indicated. It is the representative in the western hemisphere of the Old World *S. nanum* Ach. It does not resemble any other American species sufficiently to cause confusion.

DOUBTFUL SPECIES

Stereocaulon nanodes Tuck. in Suppl. II to Enum. N. A. Lichens, Am. Jour. Sci. **28**:201. 1850.

Primary thallus absent; podetia about 1 cm. tall, dendroid-branched, glabrous, more or less denuded; squamules in the form of small rounded granules, dissolving into fine, whitish powder (but not chalky as in *S. nanum*); apothecia terminal, or absent and the podetia ending in masses of soredia as *S. pileatum*.—Spores 24–42 × 2.5–3 μ.

I have examined at the Tuckerman Herbarium the type specimens of this species, collected by TUCKERMAN at Crystal Falls, Saco Falls, and upper gorge of the Ammonoosuck, in the White Mts., New Hampshire. Although not readily referable to any other species of *Stereocaulon*, I have placed this species as doubtful on account of the fact that it has apparently never been collected again in the White Mts., which is perhaps one of the most thoroughly explored regions, botanically, in North America. The only other record of this species is Newfoundland on the authority of Dr. J. W. ECKFELDT. Through the courtesy of Mr. WITMER STONE of the Philadelphia Academy of Sciences I

have had an opportunity to examine the specimens upon which this record was based. One sheet is *S. pileatum* Ach.; the other, depauperate specimens of *Cladonia decorticata* (Flke.) Spreng. The species is known, therefore, only from the type collections.

Stereocaulon ramulosum (Sw.) Ach.

In the herbarium of the Geological Survey of Canada is a sheet bearing three specimens of this species with the label: "Lichenes Boreali Americani. No. 89. Dalles, Oregon, on the earth. Legi John W. Eckfeldt. 1880." As no corresponding specimens are to be found in Dr. ECKFELDT's herbarium at the Philadelphia Academy of Sciences, and as *S. ramulosum* is not otherwise known from the United States, there has undoubtedly been some mistake in the labeling of the specimens mentioned above.

WELLESLEY COLLEGE
WELLESLEY, MASS.

BRIEFER ARTICLES

THE EPIDERMAL CHARACTERS OF FRENELOPSIS RAMOSISSIMA

(WITH TWO FIGURES)

The genus *Frenelopsis* was founded by SCHENCK in 1869[1] upon abundant material from the Wernsdorferschichten (Lower Cretaceous), and named from its resemblance to the modern genus *Frenela*. *Thuites Hoheneggeri* of ETTINGSHAUSEN was the type and only species. This was, he says, the most abundant fossil in those beds in which it occurs, and it received a careful and elaborate treatment at his hands. This species has subsequently been recognized in the Kome beds of Greenland, the Trinity beds of the Texas region, the Raritan and Magothy formations of New Jersey, and the Turonian of Bagnols, France. In 1880 HOSIUS and VAN DER MARCK described a rather illy defined species, *Frenelopsis Königii*, from the Senonian of Westphalia,[2] and the next year HEER[3] described an additional species, *F. occidentalis*, from Portugal, which SAPORTA has shown[4] ranges from the Urgonian of Cercal, through the Albian of Nazareth, into the Cenomanian of Alcantara and Padrao. The latter author also describes an additional species, *F. leptoclada*,[5] which is confined to the Lower Cretaceous of Portugal (Neocomian-Aptian).

In 1889 VELENOVSKY described the Bohemian form *F. bohemica* from the Cenomanian of that country (*op. cit.*), and the next year FONTAINE described the two species *F. ramosissima* and *F. parceramosa* from the Potomac group of Virginia, the same author three years later founding a third species, *F. varians*, upon material from the Trinity group of Texas. NEWBERRY in 1896 described a ninth species, *F. gracilis*,[6]

[1] Palaeontographica **19**:13. 1869.

[2] *Ibid.* **26**:132, 181. *pl. 37, fig. 148.* 1880.

[3] Cont. Foss. Fl. Port. 1881:21. *pl. 12, figs. 3b, 4–7.*

[4] Fl. Foss. Port. 1894: 139, 199, 214. *pl. 26, fig. 16; pl. 36, figs. 1, 2; pl. 38, figs. 2, 3; pl. 39, fig. 20.*

[5] *Ibid.* 109, 113. *pl. 19, fig. 18; pl. 21, figs. 9–11.*

[6] Fl. Amboy Clays 1896:59. *pl. 12, figs. 1–3a.*

which is a very abundant Upper Cretaceous type, and which has been recently shown by HOLLICK and JEFFREY to be unrelated to *Frenelopsis*.[7]

Although fruiting specimens have not been found, the position of the genus in the Cupressineae is not disputed at the present time, although at one time HEER argued for an affinity with *Ephedra*. The genus may be defined as follows:

Shrubs or trees with cylindrical, jointed, monopodial stems and branches, the latter of which may be alternate, apparently in a single plane, or whorl, often of large size, stems up to 5 cm. in diameter having been found in the Virginia area. Leaves much reduced, somewhat variable in outline, in general triangular with a broad base and an acute apex, squamiform, appressed, one to four at the nodes, decussate. Internodes variable in length, but longer in the apparently annual shoots, which were more or less deciduous and functioned as leaves, since the fine longitudinal striae with which their surface is ornamented turn out to be rows of stomata in certain of the species which have been examined microscopically.

It is for the purpose of describing the latter characters of this interesting American Lower Cretaceous species that the following brief note is published.

Frenelopsis ramosissima ranges from the bottom to the top of the Lower Cretaceous in the Maryland-Virginia region to which it is thus far confined. It is by far the most abundant form at the celebrated plant locality of Fredericksburg, Va. The coarse arkosic sandy clays of this age are sometimes packed with the remains of this species, with its crowded twigs and short internodes generally completely flattened, and with all of the tissues gone except the epidermis, which must have been very tough and coriaceous in life, since the preservation of these forms was largely due to its resistant nature. The cuticle of the type of the genus, *F. Hoheneggeri*, was studied by ZEILLER and described in 1882,[8] and six years later VELENOVSKY described[9] the epidermal features of *F. bohemica*. The stomata in these species were found to consist of usually four cells, although sometimes five or even six were present. These guard cells are symmetrically arranged, the opening between them being approximately in the form of a narrow-rayed star. According to the former author, they ally these forms with the existing species of *Cal-*

[7] Mem. N.Y. Bot. Gard. **23**:6. 1909.

[8] Obs. sur quelques cuticules fossiles. Ann. Sci. Nat. Bot. VI. 13:231. *pl. 11.* 1882; Eléments de paléobotanique 274. *fig. 196.* 1900.

[9] Ueber einige neue Pflanzenformen der böhmischen Kreideformation. Sitz. K. Böhm. Gesell. Wiss. Prag 1888:590. *figs. 1–3, 10.*

litris and *Libocedrus*, and effectually disprove HEER's contention that this curious genus is a member of the Gnetales allied to *Ephedra*.

In *F. ramosissima* we find a very similar arrangement to that described in the two species just mentioned. The epidermal cells are very small, the largest not exceeding 0.025 mm. in diameter, and the average being about half this size. They are roughly rectangular in shape and have very thick walls. Their most curious feature, one not observed in any

FIG. 1

other species of this genus, is the presence of minute, usually curved, spinelike outgrowths of large numbers of the epidermal cells. These protuberances vary in prominence from blunt papillae of various heights to pointed spines 0.025 mm. in length. These are not present on all of the epidermal cells, and some preparations of the epidermis are apparently entirely smooth. Fig. 1 shows a characteristic bit of the epidermis dotted with these spines. For the camera lucida drawings from which this figure was made I am indebted to Dr. FREDERICK H. BLODGETT, a former student of the Johns Hopkins University. Some of the spines, probably all of them, have a central cavity opening into the interior of the epidermal cell, which they surmount, as is shown in

one of the individual spines figured. The second and third single spines figured show irregular cavities toward the apex which are apparently cut off from the cell cavity, and the third spine figured gives a good idea of the papillose character of those adjacent cells in which these processes are not prominently developed.

In the area included in fig. 1 are three of the curious stomatal openings which apparently characterize the genus *Frenelopsis*. These are circular in outline and about 0.03 mm. in diameter. They are very numerous, but whether they are localized on certain portions of the branches which perform the functions of leaves in this genus, or whether they are uniformly distributed on the annual shoots, could not be determined. They consist of five or six guard cells arranged around the

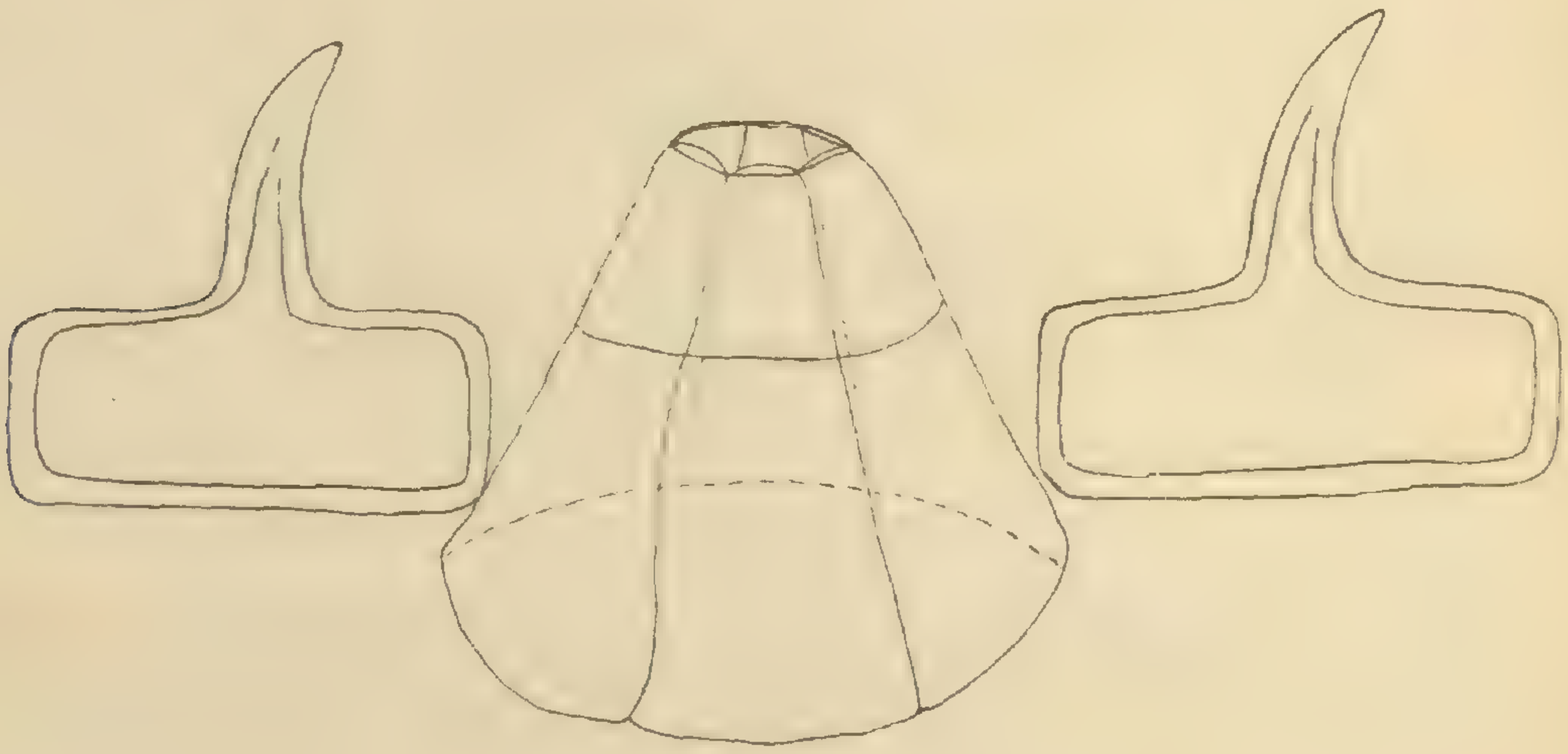


FIG. 2

central stomatal opening. These cells are much thinner-walled than the epidermal cells. In form they are relatively slender distally and broad proximally. As viewed through the microscope, they are darker colored around the stomatal opening and peripherally they are lighter. Since structural material is not available, their exact attitude is made out with difficulty. Their outer centrally directed ends come into focus at about the same time as do the outer ends of the longer spinelike processes, or very soon after, while their inner broad ends are visible after the epidermal cells have gone out of focus; hence it is obvious that they are inclined toward each other and project outward for a considerable distance from beneath the surrounding epidermal cells. It is believed that fig. 2, which is a diagrammatical drawing of a single group of these guard cells and two adjacent epidermal cells viewed in a radial section of a twig, gives an accurate idea of their arrangement and proportions.

In their more essential characters they agree with the stomata as described by ZEILLER for *F. Hoheneggeri* and by VELENOVSKY for *F. bohemica*. Just what were the physiological factors responsible for the great reduction of the leaves and the assumption of the photosynthetic processes by the branches in *Frenelopsis* it is difficult to imagine. Such features are usually associated with peculiarities of climate and habitat, and suggest strong insolation and lack of humidity; but such conditions are not suggested by the other members of the flora associated with *Frenelopsis*, since with the Potomac species are found large numbers of ferns, many of them apparently tree ferns with decompound fronds a meter or more across, and large numbers of cycads of various genera and large size; while in the latest beds in which *F. ramosissima* occurs there are considerable numbers of dicotyledonous leaves, some of which are allied with genera which in the modern flora are confined to tropical areas where the humidity is high and the rainfall heavy.

It is possible that these peculiar features in the cretaceous species of *Frenelopsis* were inherited from triassic ancestors which acquired them during those portions of the Triassic when the climate was extremely arid, as we know it was from physical as well as paleontological criteria.

—EDWARD WILBER BERRY, *The Johns Hopkins University, Baltimore, Md.*

CURRENT LITERATURE

BOOK REVIEWS

The teaching botanist

The second and revised edition of this book[1] is almost completely rewritten and is larger than the former edition by more than 60 per cent. The general plan is quite similar to that of the former book, which was reviewed in this journal eleven years ago (28:276. 1899). During the intervening years attention to the teaching of science has greatly increased; and the author has been a potent factor in stimulating a scientific attitude toward science teaching. Although the results of experiments that have been included in this volume have not furnished solutions to many of the difficult problems, some progress has been made in the direction pointed out in the introduction to the first edition, in which the author said: "The botanical course of the near future must be more adaptive to education, more broad and representative of the science, more economical of energy than in the past."

The book consists of two parts and an appendix. Part one includes nine chapters which deal with the purpose and methods of botanical teaching. It treats of such topics as the place of science in education, the kind of botany that is of most educational worth, desirable characteristics of good teaching and good teachers, the equipment and method of work in the laboratory, botanical books, etc. These discussions are of the greatest value to anyone who teaches botany, and some of the chapters will be found equally helpful to teachers of other sciences. The discussions are broad, free from a didactic attitude, and full of stimulus to new endeavor on the part of those who are engaged in teaching science. The practical suggestions regarding laboratory appliances and the purpose and means of experimentation are almost indispensable to progressive teachers.

Part two consists of "outlines and directions for a synthetic course in the science of botany." It is divided first into the "structure and function of plants," a commendable change from the former titles "the principles of the science of botany," and "natural history and classification of the groups of plants." The order of the topics within these divisions is essentially the same as in the first edition, but the outlines for work are greatly changed. They are more complete and more definite, more easily interpreted by the student, and at the same time better calculated to secure independent investigation and inference. Although the outlines purport to represent a synthetic course,

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[1] GANONG, WILLIAM F., The teaching botanist. Revised edition. pp. xi+439. *figs. 40.* New York: Macmillan. 1910.

the morphological, ecological, and physiological treatment of each topic is kept rather distinct. At times excellent work that is suggested in physiology is quite unrelated to the other work with which it appears, as when the physiology of turgidity and osmosis is interpolated under the caption of "the morphology of flowers," or the tropisms under "the morphology of fruits."

There is confessedly presented more work than can be done in a year. The teacher must adjust the course to his needs and facilities. The outline will doubtless prove most valuable in directing many teachers so that they can arrange the kind of course that best suits their needs. An appendix gives the unit statements for courses in secondary schools as they have been outlined by the special committees, one from the Botanical Society of America and the College Entrance Board, and the other from the North Central Association of Colleges and Secondary Schools. These are the two representative organizations that have attempted to outline these statements, and therefore their units should be of particular interest to botanists.

Teachers of botany and botanists in general are greatly indebted to Professor GANONG for this book, which should be influential in enhancing the educational efficiency of science and particularly of botanical science.—O. W. CALDWELL.

Tropical agriculture

Agriculture in the tropics is the title of a book[2] designed to treat chiefly of the commercial aspects of tropical plants, and is in no sense a guide to the practice of agriculture. The most valuable arable lands of the tropics are now under the control of white people, and the book obviously is intended to furnish them with data that "may be helpful and thought-stimulating for the student, administrator, or traveller." The great influence of "western" civilization and agriculture is credited with having brought a revolution in tropical agriculture.

Parts I and II ("The preliminaries to agriculture" and "The principal cultivations of the tropics") will be of interest to students of plant life, while these parts and parts III and IV ("Agriculture in the tropics" and "Agricultural organization and policy") will interest geographers and economists. Topics of special interest in part I are land and soil, climate, drainage and irrigation, and plant life in the tropics (acclimatization). In part II there are presented the leading tropical economic plants and plant products, their botanical nature, history, cultivation, productivity, use, marketability, commercial importance, adaptability to new regions, and dangers from plant and animal parasites. In part III much attention is given to the need of giving modern agricultural education to the peasants who farm the tropical estates.

The book contains an immense amount of statistical matter relative to the

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[2] WILLIS, J. C., Agriculture in the tropics; an elementary treatise. pp. xviii+222. *figs. 25*. Cambridge Biological Series. London: Cambridge University Press. $2.50.

importance of agricultural plants and their future possibilities. It will be found a valuable reference book upon many questions pertaining to economic and commercial aspects of tropical plants. Botanically, however, the book is often defective, as for example, in speaking of the growth of *Cannabis sativa* for its opium-like drug, the author says: "The male flowers are removed in November, for if the female flowers are fertilized there is no formation of the drug."—O. W. CALDWELL.

The geography of ferns

It is a praiseworthy thing for an investigator, who has devoted years to taxonomic exploration, to bring together in readable form the many things of geographic interest which he has observed. It is exactly this service which CHRIST, the well-known student of the ferns, has now performed.[3] The volume is divided into two parts, corresponding somewhat to the usual divisions of ecological and floristic geography. CHRIST regards the ferns as controlled by the same general distributional factors as the seed plants, the most noteworthy difference consisting in the pronounced tendency of ferns to be hygrophytic mesotherms. The great fern areas of the world are essentially coincident with the forest areas, very few species existing where the rainfall is less than 60 cm., and the greatest development occurring where the rainfall is over 200 cm.

The edaphic conditions under which ferns live are first noted, attention being called to the fact that most species are humus forms, and but slightly dependent on the mineral nature of the soil. Under the head of climatic conditions, a number of characteristic fern formations are described. The hygrophytic ferns are treated at considerable length, especial attention being devoted to the epiphytic forms. The features of the xerophytic ferns are well portrayed. In the floristic part of the work, consideration is given to a number of cosmopolites, and also to endemic forms and to species with disconnected areas. The body of the second part is made up of the treatment of the floristic regions of the world. Here, as elsewhere in the volume, the author makes it very clear that the ferns, in spite of their great age, are far from being a senescent group.

The volume is a mine of information, and will be of the highest value to all botanists. The excellent index makes it possible to find at once the known ecological and geographic facts concerning most living ferns.—HENRY C. COWLES.

An organic chemistry

The third English edition of HOLLEMAN'S *Organic chemistry* has just appeared,[4] edited by A. JAMIESON WALKER. The value of the book as a text

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[3] CHRIST, H., Die Geographie der Farne. 8vo. pp. 358, with frontispiece, *figs. 129* (mostly photographic reproductions), and *3 maps*. Jena: Gustav Fischer. 1910.

[4] HOLLEMAN, A. F., A textbook of organic chemistry. 8vo. pp. xx+599. *figs. 80*. New York: John Wiley & Sons. 1910.

is shown by a statement from the author's preface: "Besides the four editions of the original Dutch volume and three in English, seven editions of this book have been published in German, two in Russian, two in Italian, and one in Polish. A French edition and a Japanese edition are also in preparation.' A second quotation from the preface gives the aim of the book, which is well carried out, and it gives the text its great value as a general reference book' for students of physiology. "Most of the short textbooks of organic chemistry contain a great number of isolated facts; the number of compounds described in them is so considerable as to confuse the beginner. Moreover, the theoretical grounds on which this division of the science is based are often kept in the background; for example, the proofs given of the constitutional formulae frequently leave much to be desired. However useful these books may be for reference, they are often ill-suited for textbooks, as many students have learned from their own experience."

The chapters on sugars, amino acids, and proteins, of the greatest direct interest to physiologists, though brief, are certainly clear statements of the fundamental facts of the chemistry of these bodies. The chapter on proteins is in the body of the book just after amino acids, instead of in an appendix, as it appeared in the second edition. WALKER is credited with having introduced into the book the protein classification adopted by the Chemical Society of London, the English Physiological Society, the American Physiological Society, and the American Society of Biological Chemistry.—WILLIAM CROCKER.

NOTES FOR STUDENTS

Magazines for students of genetics.—The era of experimental study in heredity and evolution has called for new publications devoted to the results of research in this field. While all the biological journals occasionally contain articles which are of interest to the student of experimental evolution, several special magazines have been established which are quite indispensable to anyone who wishes to keep reasonably well informed regarding current progress in genetics and related subjects.

The first of these which deserves mention is *Biometrika*, which was established in London in 1901 under the editorship of Professor KARL PEARSON, for the publication of papers on mathematical methods of dealing with variation, heredity, selection, etc., and the results of their application. While not many of the articles published in *Biometrika* deal strictly with genetics, it was the first journal to voice the demands for more exact methods of investigating problems of evolution, and as the whole trend of modern biology is toward the greater exactness involved in mathematical treatment of biological data, *Biometrika* should continue to fill an increasingly important place, notwithstanding the unfortunate fact that there is a tendency of late to allow personal feeling to dominate both the policy of the magazine and the attitude

of many prominent students of genetics toward it and the methods it advocates.

The second magazine which is devoted specifically to evolution and related subjects is the *Archiv für Rassen- und Gesellschafts-Biologie*, edited and published in München by Dr. A. PLOETZ, assisted by Dr. L. PLATE and several others. This magazine was established in 1904, just at the time when interest in evolution was being revived by the general introduction of the new methods. It is not wholly occupied with the results of experimentation, but contains besides these many philosophical and more or less academic discussions, which give it the flavor of transition from the older evolutionary literature of the post-Darwinian writers to the new type of literature introduced and exemplified by the work of DE VRIES and MENDEL.

In 1908 a new monthly German magazine entitled *Zeitschrift für Induktive Abstammungs- und Vererbungslehre* was established in Berlin under the editorship of Dr. E. BAUR, assisted by Drs. CORRENS, HECKER, STEINMANN, and WETTSTEIN. This magazine is at the present time the most valuable of all similar journals, as it offers in excellent form a large volume of original matter, adequate abstracts from a large proportion of the papers on the same subjects published in other journals, and finally gives a very complete classified list of new literature dealing with the same subjects. This journal is absolutely indispensable to all who wish to investigate problems of heredity, variation, and evolution.

In October 1909 a journal first made its appearance in London entitled the *Mendel Journal*, which is unique in a number of particulars. In the first place, its editorship is entirely anonymous, though many internal evidences leave little doubt as to the source of the dominating influence. It seems to be in a sense the organ of the Mendel Society of London, as it publishes the various addresses made before that body. While this journal has a number of interesting papers which supply valuable data, especially on human inheritance, its whole attitude is one much to be regretted. The express object of the magazine is to furnish a *propaganda* for Mendelism. It represents the "Mendelians" as an army which is fighting an opposing army, the "Biometricians," and makes many unwarranted slurring attacks upon Professor PEARSON and those who have assisted him in working out the biometrical methods of dealing with biological data. No true scientist can fail to deprecate the introduction of propagandism and personal enmity into science. It may be expected that the publication of such a journal will act as a boomerang, and will do the cause of Mendelian investigation a distinct injury. The aim should be simply to arrive at the truth and not to adopt and establish a creed to be forced upon others who cannot be convinced of the truth by the data presented. Like *Biometrika*, the *Mendel Journal* has no regular periodicity, but its appearance is promised whenever sufficient material is at hand.

In America the demand for journals dealing with genetics has brought á most satisfactory response from the *American Naturalist*, which about two

years ago, under the editorship of Dr. J. McK. CATTELL, adopted as a general policy a specialization upon evolutionary topics. The American Society of Naturalists chose for itself the same field, and the *American Naturalist* is in a certain sense the organ of that society.

The last arrival in the field is the new magazine issued by the American Breeders' Association, and known as the *American Breeders' Magazine*, published in Washington under the editorship of the secretary of the Association, W. M. HAYS, assisted by the secretaries of the Plant and Animal Sections, N. E. HANSEN and H. W. MUMFORD. The first issue of this magazine has just appeared, and gives every evidence of its intention to take a dignified place among economic journals, and a modest and unassuming place among scientific magazines, thus correctly representing the unique position of the Association whose organ it is. The *American Breeders' Magazine* is being issued as a quarterly, but it is hoped by those who have it in charge that it may soon be changed to a monthly magazine. The opening number presents as a frontispiece a portrait of CHARLES DARWIN, and also gives portraits of GREGOR MENDEL and AMOS CRUIKSHANK, the latter the originator of the shorthorn cattle, and said to be the first to utilize fully the discovery of a mutation in the establishing of an important economic breed. Besides brief biographical sketches of these three men, this first issue presents papers on "Increasing protein or fat in corn," by L. H. SMITH; "New methods of plant-breeding," by GEORGE W. OLIVER; "The army horse," by CARLOS GUERRERO; "Imperfection of dominance," by C. B. DAVENPORT; "Poultry-breeding in South Australia," by D. F. LOWREY; and several articles on the breeding of deer and other wild animals by D. E. LANCE and other members of the committee on breeding wild animals. As it is the plan of the American Breeders' Association to continue the publication of its *Year Book*, the issue of this magazine will make it even more important that all those who are engaged in investigation or who are interested in matters involving genetics should become members of the Association and thus secure its publications.—GEO. H. SHULL.

Respiration.—PALLADIN[5] has tested the effect of several poisons on the CO_2 output from living plant organs and from similar tissues that have been killed by freezing for several hours. He finds that 0.09 per cent quinine hydrogen chlorid more than triples the CO_2 output from living stem tips of *Vicia Faba*, while it does not affect the killed ones; 0.05 per cent was far less effective on the living tissue and indifferent in the dead; and 1.0 per cent tripled the product from the living and reduced it markedly in the dead tissue. In the living bulbs of *Gladiolus Lemonia*, 8 cc. of ether per 7.5 liters of air

[5] PALLADIN, W., Ueber die Wirkung von Giften auf die Atmung lebender und abgetöteter Pflanzen, sowie auf Atmungenzyme. Jahrb. Wiss. Bot. **47**:431–461. 1910.

doubled the CO_2 production, while 16 cc. in the same volume was less effective. Neither increased the output from killed bulbs. Ether gave little stimulation in the living bulbs of *Gladiolus Colvillii* and *Allium Cepa*, while it cut greatly the output from dead tissues. Arbutin (1 and 2 per cent) reduced considerably the CO_2 yield from live wheat seedlings, and very markedly that from killed ones. PALLADIN finds that the stimulative or inhibitory effect of poisons on the living tissues was not accompanied by an increase or decrease in peroxidase, but the decreased output from dead tissues was accompanied by a decrease in peroxidase. The stimulatory effect of poisons gradually disappears and toxic results soon set in if the surrounding atmosphere is displaced by hydrogen. Extreme temperatures also reverse the effect of the poisons. The author believes that the increased CO_2 output in the living tissues is a result of their battling against the poison, and that the ability to do battle is lost with death or with unfavorable life conditions. He concludes that the action of poisons on the respiration of dead tissues is a direct result of injury to the respiratory enzymes, while their action on living plants is indirect through the living protoplasm.

PALLADIN believes that the increased respiration is due to an increased transformation of the zymogens to active enzymes, which is also accompanied by an increased destruction of the active enzymes. For this reason the stimulated plant shows no increase in active enzymes over the control. One feels that this conclusion is not sufficiently backed by evidence.

PALLADIN[6] has also attempted to ascertain the effect of contained lipoids upon the respiration of plant tissues. This he did by extracting dried wheat seedlings for two hours with various lipoid solvents (toluol acetone, benzen, chloroform, benzin, alcohol, etc.). In general he finds that the more lipoid and therefore phosphorus-containing material the solvent extracts, the more it reduces respiration. He believes this is related to the important rôle of phosphates in zymase action. He finds, however, that the amount of reduction in respiration is not exactly proportional to the amount of lipoid extracted. He explains this in part by the fact that different solvents will extract not only different amounts, but different sorts of lipoids. In substance he also says: "When we separate the lipoids we destroy the normal protoplasmic structure. We separate from the protoplasm the cement which binds its heterogeneous parts into a whole. I have shown that even the mechanical breaking up of the plasma structure reduces very markedly the respiration of the plant tissue." He points out various other means through which these solvents may affect the respiration, such as the coagulation by alcohol. With other authors, he believes the lipoids are to be considered intermediary bodies in respiration, that is, oxygen-carriers. He would list them with his respiratory chromogens. One gets the impression that PALLADIN feels himself much more secure than he should when treading on such uncertain ground.

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[6] PALLADIN, W., Zur Physiologie der Lipoide. Ber. Deutsch. Bot. Gesell. 28:120–125. 1910.

GALITZKY and WASSILJEFF[7] have studied the effect of boiled extract of wheat and bean seeds upon the respiration of living and killed (by treatment with acetone) wheat seedlings. In agreement with various other workers, they find that the extracts greatly increase the CO_2 output in both living and killed seedlings: 60 per cent in normally acid cultures, 117 per cent in neutral cultures, and 86 per cent in slightly alkaline cultures. The authors raise the question, "Is the stimulative action due to food materials supplied by the extract, or to bodies of the nature of co-enzymes?" L. and N. IWANOFF have assumed that the stimulation is due to the action of organic or inorganic phosphates on anaerobic respiration, analogous to the action of these bodies as co-enzymes for zymase. The authors find that peptone, glycerin, mannit, sodium lactate, quinic acid, sodium chlorid, and ferric chlorid have very little or no effect upon the respiration of the seedlings. Dextrose, saccharose, maltose, and sodium carbonate give a slightly increased CO_2 output, about 20 per cent. Arabinose and ferrous sulfate give a somewhat greater stimulation of the extracts. The authors consider it especially interesting that probable intermediate products of alcoholic fermentation, lactic acid and sodium lactate, have no stimulative effect. This is quite in contrast with conceptions of KOSTYTSCHEW. The authors are to extend the tests to various other substances, especially to phosphates, to see whether they will give the amount of stimulation shown by the extracts. One naturally wonders to what extent bacterial action may increase the CO_2 output. So far as methods are described, one certainly cannot be assured that such has not happened.—WILLIAM CROCKER.

Heliotropism and geotropism.—GUTTENBERG[8] has already shown, contrary to the earlier conception of most writers, that the effect of the geotropic stimulus is not annulled by the light stimulus, but that light of such intensity can be chosen that, when it strikes a horizontally placed orthotropic epicotyl from below, its joint action with gravity will, after various nutations, lead to the epicotyl permanently growing in the horizontal position. Compensation (placement at 45 above the horizontal) likewise results when the light of proper intensity strikes the vertical epicotyl horizontally. The intensity of light demanded to compensate gravity varies greatly with different epicotyls; while occasionally greater than one candle power, it is generally only a fraction of a candle power. RICHTER[9] called the results of GUTTENBERG into question,

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[7] GALITZKY, KATHERINE, und WASSILJEFF, VERA, Zur Atmung der Weizenkeime. Ber. Deutsch. Bot. Gesell. **28**:182–187. 1910.

[8] GUTTENBERG, H. R. v. Ueber das Zusammenwirken von Heliotropismus und Geotropismus in parallelotropen Pflanzenteilen. Jahrb. Wiss. Bot. **45**:193–231. 1907.

[9] RICHTER, O., Ueber das Zusammenwirken von Heliotropismus und Geotropismus. Jahrb. Wiss. Bot. **46**:481–502. 1909.

maintaining that the results were modified by the gaseous impurities of the laboratory in which they were obtained. GUTTENBERG,[10] on repeating his experiments in pure air, finds essentially the same compensatory values of light as he found in his earlier work. GUTTENBERG used the seedlings of *Avena* and *Brassica*, forms much less sensitive to impurities than are legumes, with which RICHTER worked. GUTTENBERG finds in *Vicia sativa*, contrary to RICHTER, that laboratory air does not increase the heliotropic sensitiveness, but in agreement with RICHTER he finds the geotropic irritability lessened. On this point, GUTTENBERG'S experiments are much more critical than RICHTER'S.—WILLIAM CROCKER.

Morphology of Phylloglossum.—A recent paper by WERNHAM[11] represent, a type, at the moment becoming much too common, in which a small basis of imperfectly examined facts is made to serve for large conclusions which are neither clearly nor logically drawn. The author has examined by means of serial sections the anatomy of two specimens of *Phylloglossum Drummondii*. He concludes that the basal leaves of this species (the protophylls of certain authors) are microphyllous, although superficially relatively large in sizes because their traces leave the stele without leaving any gap, as is the case with the Lycopsida. Concerning the relation of the sporophyll traces to the vascular system of the axis, the account is very obscure, since it is not made clear whether gaps are or are not present. The most remarkable feature of the article is the interpretation of the larger strand which passes off from the crown of the functional tuber toward the tuber of the succeeding year as a leaf trace. It has been regarded by other observers, apparently with good reason, as a branch supply, and the present author adduces apparently no valid evidence why this view of its nature should not continue to be held. On the basis of this imaginative interpretation, he comes to the conclusion that *Phylloglossum* was originally a megaphyllous form, which has become much reduced. It would be possible to prove almost anything with such reasoning as this. It seems highly desirable that morphologists should avoid eccentric conclusions of the nature illustrated by the article here reviewed. Obviously, conclusions of permanent value in regard to leaves or other organs can be reached only in the case where there is no room for doubt as to the morphological category of the structure under discussion.—E. C. JEFFREY.

Classification of conifers.—A new classification of conifers, based upon morphology, geographical distribution, and geological history, is proposed

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[10] GUTTENBERG, H. R. v., Ueber das Zusammenwirken von Geotropismus und Heliotropismus und die tropistische Empfindlichkeit in reiner und unreiner Luft. Jahrb. Wiss. Bot. **37**:467–492. 1910.

[11] WERNHAM, H. F., The morphology of *Phylloglossum Drummondii*. Annals of Botany **24**:335–347. *figs. 8*. 1910.

by VIERHAPPER.[12] It is assumed at the outset that a group whose members have in common such striking characters must be monophyletic. The morphology is confined to the grosser taxonomic characters (but includes the structure of the wood), excluding entirely the gametophytic structures, because the new system is based upon facts, and the gametophytes are not yet known in all the genera, and presumably are not yet worthy of recognition among the established facts. The obvious characters are analyzed and classified as primitive and secondary.

The Cordaitinae are the primitive stock, which during the Carboniferous gave rise to the Coniferae, the Taxocupressaceae arising as an offshoot from Ginkgoinae, and the Abietaceae coming directly from the Cordaitinae. The Taxocupressaceae include the Taxoideae and Taxodioideae arising independently from the *Ginkgo* stock during the Carboniferous, and the Cupressoideae arising during the Trias from the Taxodioideae. The Abietaceae include the Araucarioideae coming directly from the *Cordaites* stock, and the Cunninghamioideae and Abietoideae arising from the araucarian stock during the Trias.

Without commenting upon the scheme itself, it would seem to the reviewer that so much is now known about the gametophytes, and that so much of this comparatively recent knowledge is extremely significant, that it must be considered in any classification which claims to represent the phylogeny of a group.—CHARLES J. CHAMBERLAIN.

Cretaceous pine leaves.—In the communication cited the authors describe the anatomy of a species of *Pinus* and a supposed species of *Prepinus*, from the Upper Cretaceous of Hokkaido, Japan.[13] The pine leaf, denoted by the specific name *P. yezoensis*, from the description given is not very different in structure from the living *P. Bungeana* of China, since it is a soft pine with a single foliar bundle and apparently a three-leaved fascicle. In type it clearly differs from the pine leaves of the Lower Cretaceous described by the reviewer, in possessing a degenerate transfusion sheath, a well-marked endodermis, and infolded mesophyll cells. In other words, it is practically indistinguishable in its general structure from the leaf of a living pine. Interestingly enough, in a communication from the reviewer's laboratory, shortly to appear, it will be shown that the wood of a pine from the American Upper Cretaceous likewise resembles more nearly the secondary xylem of living pines than that of pines from the Lower Cretaceous. It will thus apparently be possible to distinguish between these two horizons by means of the nature of the pine flora. The *Prepinus* described, *P. japonicus* (why not *P. japonica?*), appar-

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[12] VIERHAPPER, F., Entwurf eines neuen Systemes der Coniferen. Abhandl. K. K. Zool.-Bot. Gesell. Wien **5**:1–56. 1910.

[13] STOPES, MARIE C., and KERSHAW, E. M., The anatomy of cretaceous pine leaves. Annals of Botany **24**:395–402. *pls. 27, 28.* 1910.

ently does not belong to that genus at all, since it is without the very striking internal transfusion sheath of the lower cretaceous genus, has a double instead of a single foliar bundle (a point of great importance, as will be recognized by those versed in the anatomy of *Pinus* in its living species), and no centripetal xylem. The authors make light of the absence of the last feature, but in this they are apparently not well advised.—E. C. JEFFREY.

Conduction of stimulus.—ROTHERT has shown that the conduction of stimulus of unilateral illumination from the tip of the *Avena* seedling to the darkened basal portion occurs when the vascular strands are cut; and that a horizontal incision on one side, whether toward, away, or on the flank in reference to the one-sided illumination, still permits conduction. FITTING showed that when the incision was away from the light and a mica plate inserted, no conduction occurred. The insertion of a slice of rattan in the same position did not prevent conduction; the latter of course allows the continuity of water and solution. When the mica plate was inserted in an incision on the lighted side, conduction was not hindered. JENSEN[14] finds that with the incision away from the light, no conduction occurs in dry air or in water. He assumes that under favorable conditions the stimulus can be conducted across the wound while under unfavorable conditions it cannot. In saturated air the stimulus was also conducted from the tip to the darkened base, even after the tip (1 cm. long) had been entirely cut off and set back and fastened by gelatin and cocoa butter.—WILLIAM CROCKER.

Embryo sac of Pandanus.—In 1909 CAMPBELL published an account of the embryo sac of *Pandanus*, which was reviewed in this journal (**47**:485. 1909). In this Javanese material the fertilization stage was not secured, so that it was not certain that the interesting situation described is the one at fertilization. Now there has come to hand additional material (*P. coronatus*) which has supplied the missing stage.[15] An ordinary egg apparatus is organized, but there occurs "a large discoidal mass of cells" at the antipodal end of the sac, and fusions of "polar" nuclei (up to six) were observed. The number of cells in the sac at the fertilization stage would thus seem to be greater than that recorded for any other angiosperm. The amount of antipodal tissue suggests the situation in *Sparganium*, the difference being that in the latter genus this tissue develops after fertilization.—J. M. C.

---

[14] JENSEN, P. BOYSEN, Ueber die Leitung des phototropischen Reizes in Avenakumpflanzen. **Ber. Bot. Gesell. 28**:118–120. 1910.

[15] CAMPBELL, DOUGLAS H., The embryo sac of *Pandanus coronatus*. Bull. Torr. Bot. Club **24**:293–295. *figs. 6.* 1910.

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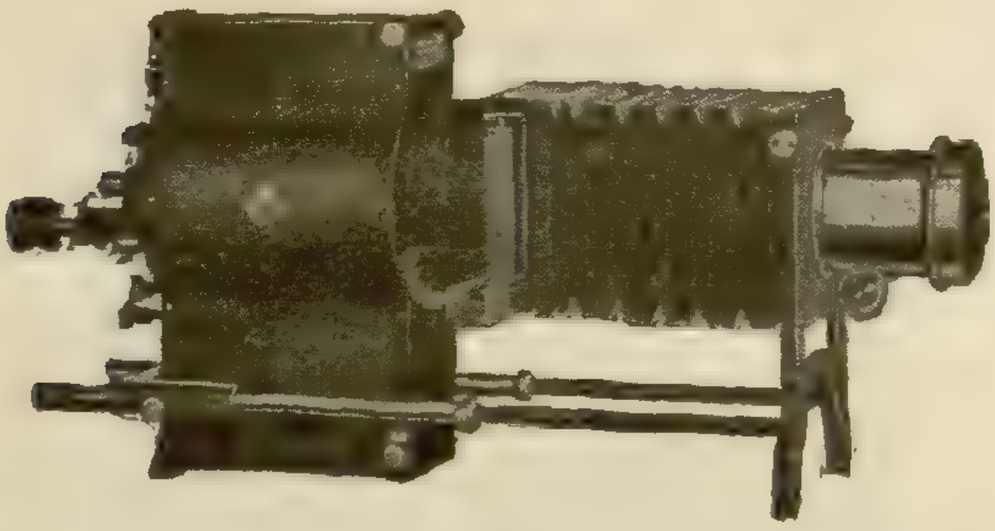

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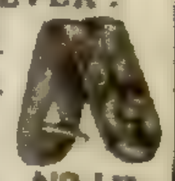

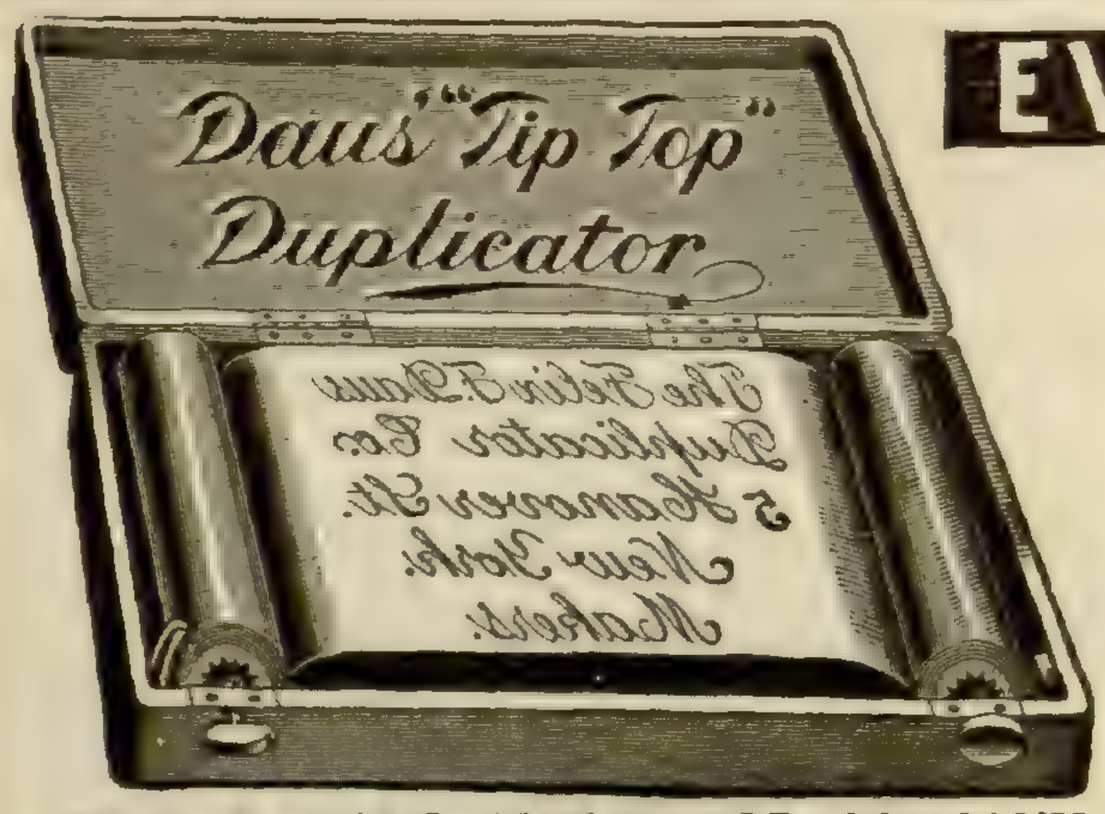

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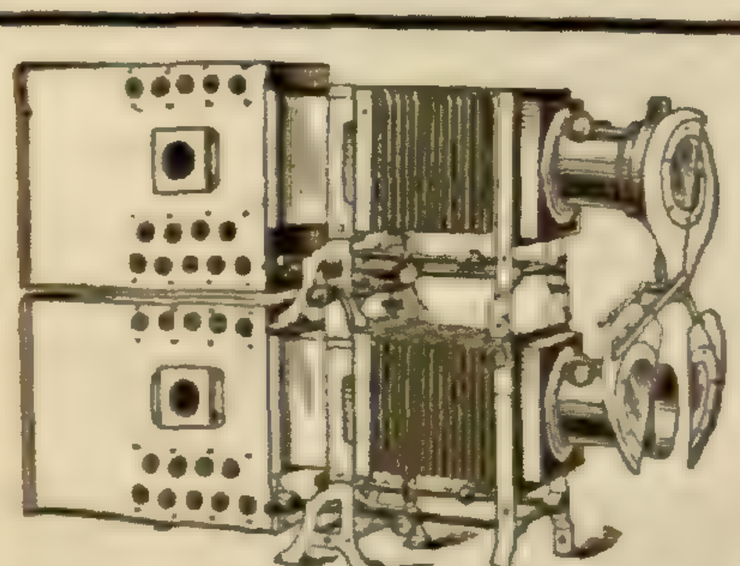

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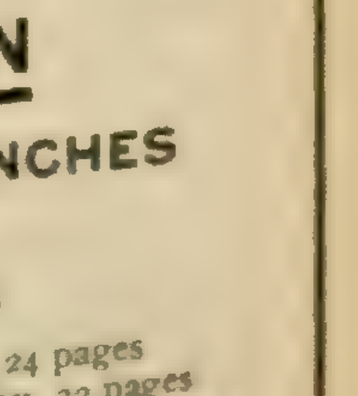

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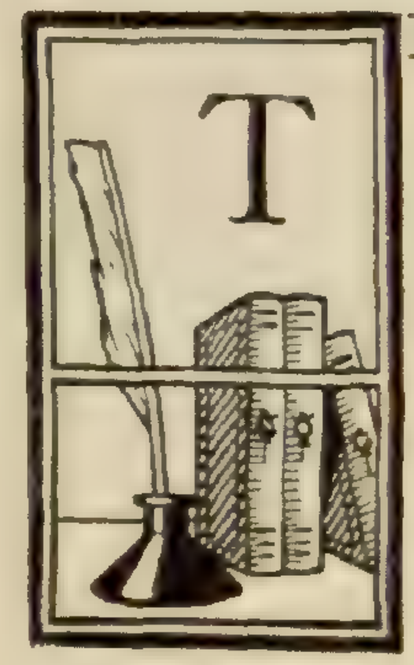

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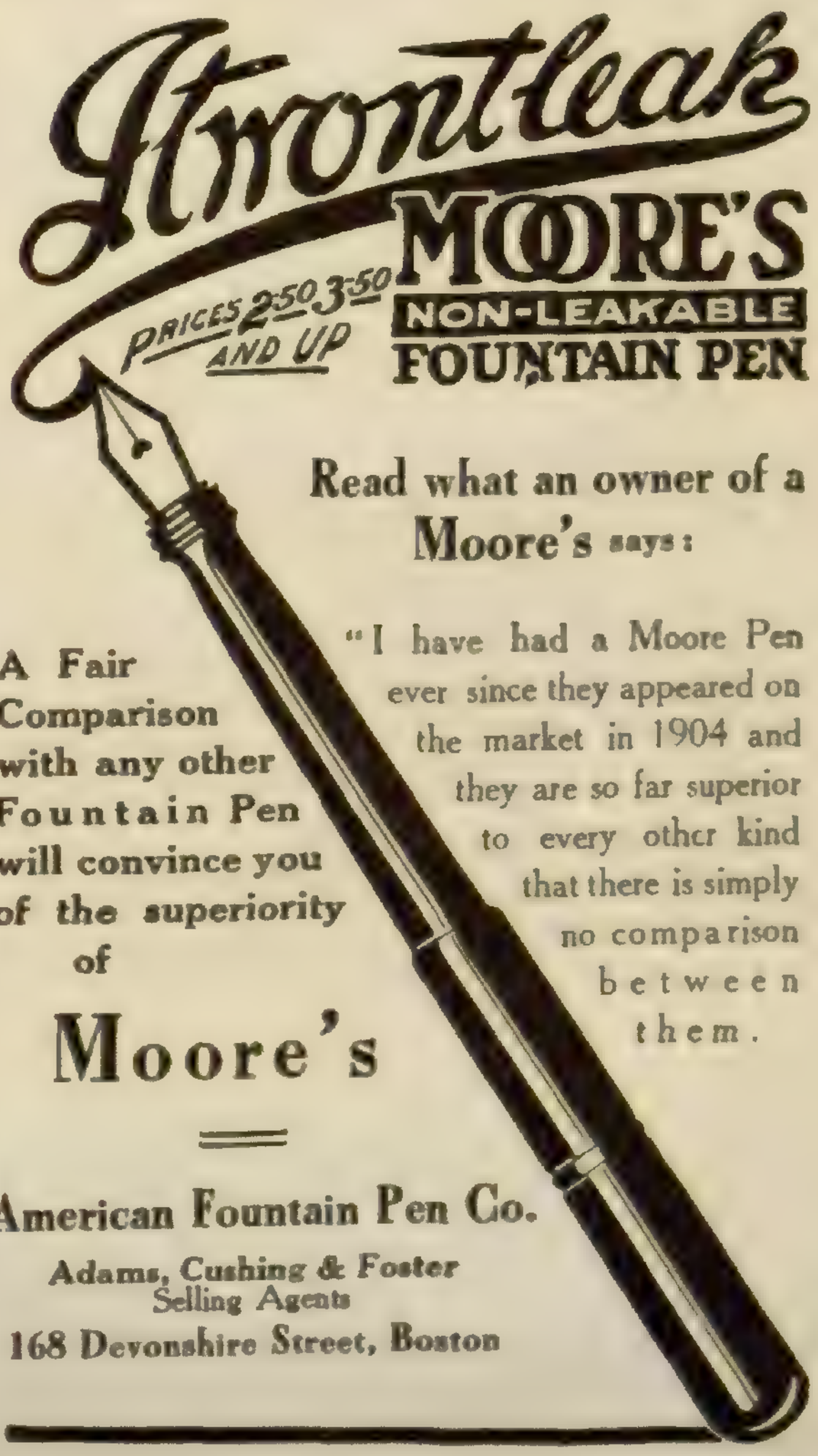

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NOVEMBER 1910

THE PEG OF THE CUCURBITACEAE

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 140

WILLIAM CROCKER, LEE I. KNIGHT, AND EDITH ROBERTS

(WITH SIX FIGURES)

Historical

The peg of seedling Cucurbitaceae has frequently been used as a marked case of adaptation to a peculiar function. It holds the seed coat while the elongating arms of the arch of the hypocotyl

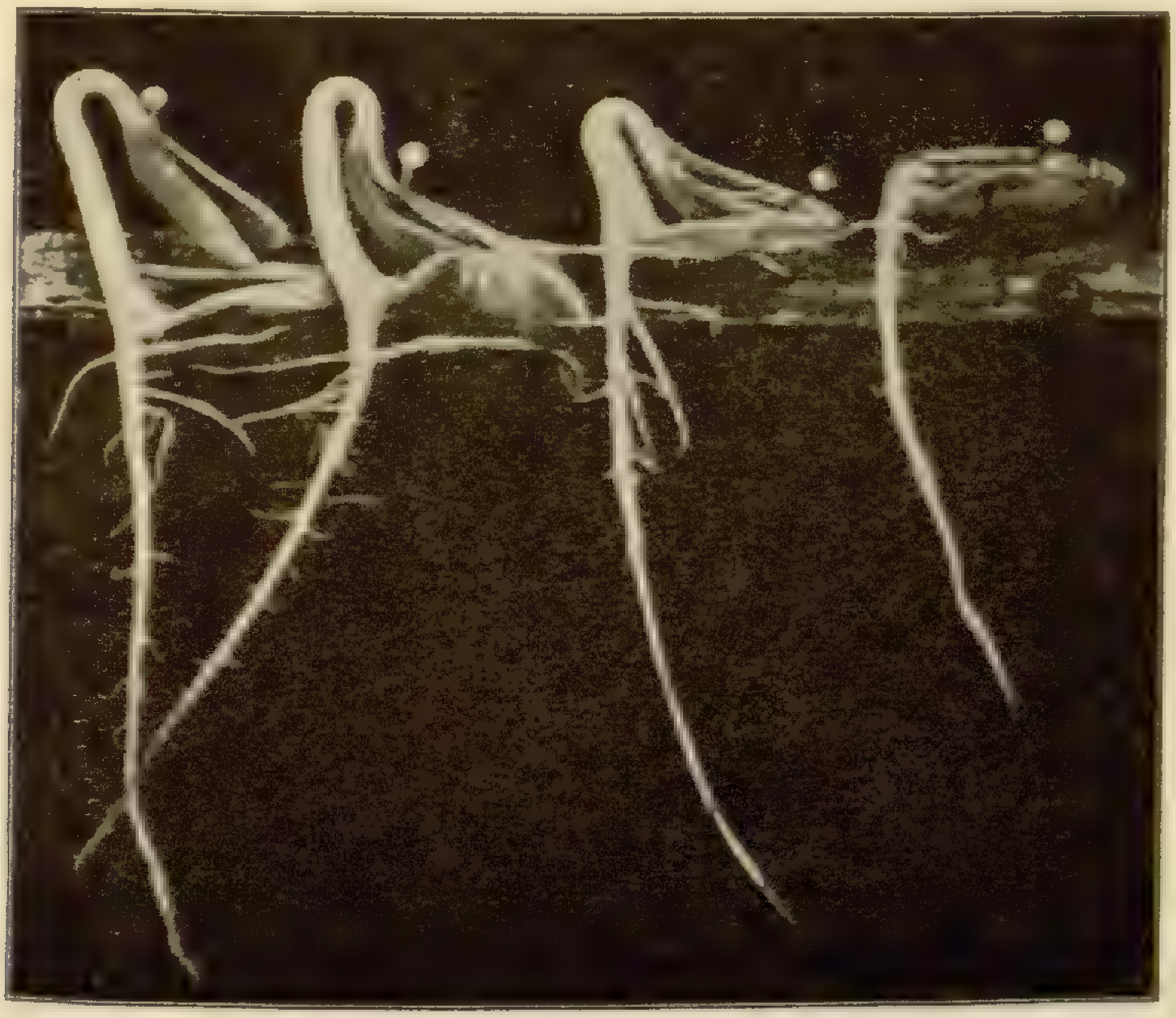

FIG. 1.—Big Tom, showing the pegs functioning in the removal of the coats.

withdraw the cotyledons from the coat. The method by which the peg functions is well shown in fig. 1.

MIRBEL[1] and TITTMAN[2] very early showed the presence of this organ throughout the Cucurbitaceae. While it is well developed in the epigean forms, it is very rudimentary in the hypogean forms, such as *Megarhiza californica* and *Sicyosperma gracilis*. The organ is by no means limited to the Cucurbitaceae, but appears in various genera of a number of families: *Mirabilis*, *Oxybaphus*, and *Abronia* (Nyctaginaceae), *Martynia* (Martyniaceae), *Lindheimera* (Compositae), *Mimosa* (Leguminosae), *Tribulus* (Zygophyllaceae), *Eucalyptus* (Myrtaceae), *Cuphea* (Lythraceae), etc. While in Cucurbitaceae the peg appears only after germination has progressed considerably, in other forms, as *Eucalyptus* and *Cuphea*, it is already laid down as a complete ring in the mature seed, and with germination completes its development.

TITTMAN recognized the biological significance of this organ in the Cucurbitaceae, and showed that it appears only on the lower side of the developing hypocotyl.

TSCHERNING[3] gives a rather full description of its histology and physiology. He states that it is a parenchymatous outgrowth. While the greater diameter of the parenchymatous cells in other parts of the hypocotyl is longitudinal, in the peg zone it is radial. The number of layers of cortical cells is also somewhat greater at the peg zone. TSCHERNING describes the effect of the position of the seed during germination upon the development and functioning of the peg. He says that when the radicle points vertically downward the swelling does not occur, and the cotyledons push above the ground still bearing the coat. With radicle pointing vertically upward, the peg develops on the concave side of the arch, but does not remove the coat. When the seeds are planted on edge, the peg develops on the concave side of the arch and wedges between the two valves of the coat, thus succeeding in removing a considerable percentage of them. When the seeds are planted on a flat face, the peg develops on the concave side of the arch and attaches itself securely to the lower valve of the coat, thereby insuring its removal. TSCHERNING emphasizes the development of the peg on the concave side of the arch, and speaks of it as a lateral pushing out of the cells due to the inhibition in the

[1, 2, 3] See under NOLL, footnote 8.

elongation on the concave side of the hypocotyl. While his relating its place of development entirely to the arch is probably correct, as we shall see later, his view as to how the arch brings about such a placement is crude. We shall see also that his claim that the peg does not develop when the seed grows with the radicle pointing vertically downward is incorrect.

FLAHAULT[4] claimed that seedlings that developed when the removal of the coats occurred in the normal way were far superior to those in which it was prevented by breaking away a portion of the lower valve of the coat so that the foot could not get a hold. This advantage he attributes of course to the hindering of assimilation by the retained coats. He claimed that the peg develops at any point on the hypocotyl necessary to enable it to hold the coat.

CHARLES DARWIN,[5] contrary to FLAHAULT, found that the peg develops only at the zone between root and stem. The lower face is root, as shown by the presence of root hairs and reaction to potassium permanganate, while the upper face is stem. DARWIN described a number of experiments, similar to those of TSCHERNING, testing the effect of the position of the seed upon the development and functioning of the peg. While DARWIN clearly showed that the peg is located at the border between root and stem, he did not show the stimuli involved in its lateral placement.

FRANCIS DARWIN[6] later showed that seedlings of *Cucurbita ovifera*, allowed to germinate on a slowly rotating clinostat with a horizontal axis, gave pegs completely surrounding the hypocotyl and approximately equal on all faces. He concluded, from the inadequate experiments of his father and himself, that gravity is a direct stimulus determining the lateral distribution of the peg, and that therefore this experiment shows that gravity is continually effective on the clinostat and only equalized in its action on the several flanks of the exposed object. The conclusion concerning

[4] FLAHAULT, C., Sur le talon de la tigelle de quelques Dicotylédones. Bull. Soc. France **24**: 200. 1877.

[5] DARWIN, CHARLES and FRANCIS, The power of movement in plants. pp. 102–107. New York. 1892.

[6] DARWIN, F., and ACTON, E. H., Practical physiology of plants. pp. 192 ff. Cambridge. 1895.

the nature of the effect of the clinostat is correct, as shown by FITTING[7] and others, but the assumption that this experiment proves it is quite another question, and, as we shall show later, quite out of accord with a number of other facts.

NOLL[8] mentioned the fact that FRANCIS DARWIN'S conclusion that gravity is a direct stimulus in determining the lateral distribution of the peg is not proved by his meager experiments. He also claimed that only 50 per cent or less of the seedlings grown on a clinostat produce ringlike pegs, while the remainder show sharp arching, with a one-sided peg. NOLL stated that all flanks of the hypocotyl are qualitatively equally capable of peg-development, but that quantitatively the broader flanks produce the larger peg. He concluded that contact of the seed coats is not a necessary stimulus to peg-development, for the peg still appears when the coats are removed. The contact of the coat, however, increases the size of the peg. He performed a number of experiments in which seeds were germinated with the two opposite broad faces exposed to gravity alternately and for equal periods. In all these cases the two faces developed essentially equal pegs. He especially emphasized these as showing that the peg stands in strong relation to gravity and owes its stimulus for formation to gravity. Many experiments were also performed in which seedlings were grown with the radicle directed perpendicularly downward or at a slight deviation from this position. From these he concluded that the gravity stimulus reaches beyond the lower pole of the seedling axis. At a deviation of 5° from the vertical he found a weak peg on the upper side, while at 7°.5 the peg was almost exclusively on the lower side. He fixed the limit of the field of stimulation at 6°–8° deviation from the vertical. He specified that these are to be taken only as approximate figures and as applying to *Cucurbita Pepo*. In two seedlings slight pegs were found on the upper side at a deviation of 8°. Seedlings were also found that showed no peg, but he did not know how to account for this. On account of great variation in response, NOLL empha-

[7] FITTING, HANS, Jahrb. Wiss. Bot. **45**:575–600. 1909.

[8] NOLL, F., Zur Keimungs-Physiologie der Cucurbitaceen. Landwirt. Jahrb. **30**:145–165. 1901.

sized that reliable conclusions can be drawn only by the employment of a large number of seedlings in each culture.

It is evident that both FRANCIS DARWIN and NOLL considered gravity as well as the arching of the hypocotyl as direct stimuli in determining the lateral distribution of the peg. NOLL says (p. 164): "Die meiste inseitige Ausbildung des Wulstes tritt als Ergebnis zweier heterogener Reize ein. Die localisierte Entstehung des Wulstes ist einerseits abhängig vom Gravitationsreiz. Der Wulst bildet sich auf der jeweiligen Unterseite. . . . . Die einseitige Wulstbildung wird andererseits auch bedingt durch die Krummung des Mutterorgans, derart, dass auf der Konkavseite die Bildung des Stemmorgans ausgelöst wird."

FRANCIS DARWIN[9] has lately used the peg of the cucurbits as a mainstay for the memory theory of plant response. In this, of course, he assumed that its development and position are directly determined by gravity. Whether gravity acts as a direct stimulus to its production and placement is the principal question to be tested by the following experiments.

Methods and materials

NOLL failed to control the factors involved in this problem in a way that enabled him to determine the part played by each in the lateral placement of the peg. He apparently failed to notice the potency of contact of the coats on the one hand, and of the media on the other, in arch-production. In the experiments here given, to avoid this important influence, except when its effect was to be studied, the seeds, whether on the clinostat, centrifuge, or in rest positions of different inclinations, were freed from the coats at the tips and each held by two pieces of cork between which the cotyledons were clasped at the central region. The whole apparatus was kept in the dark and watered by a very fine spray heated to 23° C. The spray was formed by forcing the water by means of tap pressure through a tank of considerable size kept in a water bath at constant temperature, and allowing it to break against a plate of glass. In this way contact of both the coats and the soil media is entirely eliminated. Contact, as data later given will

[9] DARWIN, FRANCIS, New Phytologist **5**:199–207. 1906.

show, is a very important influence. We are unable to see how NOLL could get results at all dependable without taking this precaution. He was always studying the effect of two stimuli when his results purport to be considering one.

The seeds used in this work were obtained from VAUGHAN and will be mentioned by the trade name used by that dealer.

Experiments and discussion

EFFECT OF CONTACT OF COATS

As has been stated, the contact of coats plays a very important part in arch-production, and therefore indirectly upon the lateral

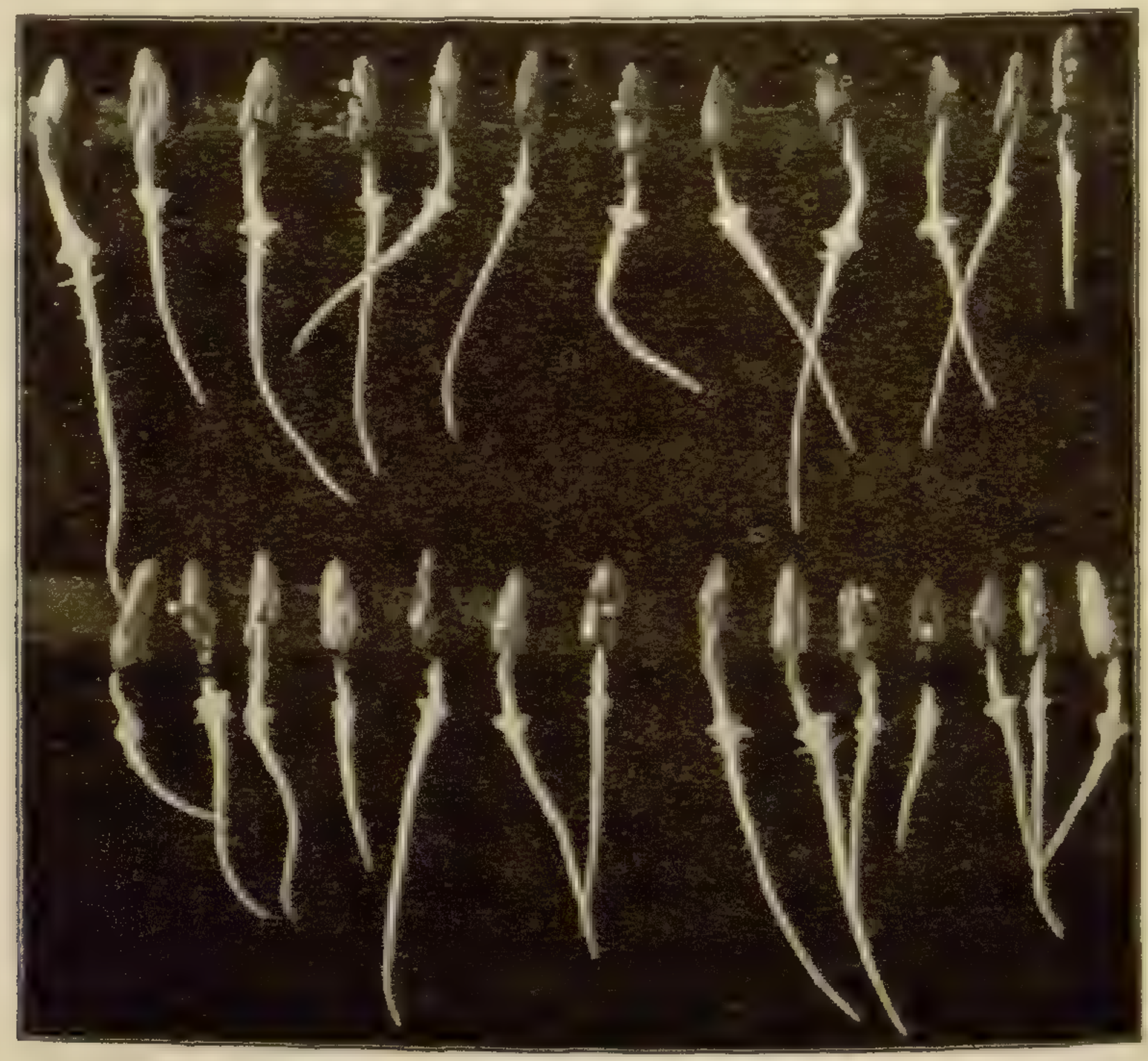

FIG. 2.—Crop of Hubbard squash grown in spray at 23° C.; coats removed at the tip and radicles pointing downward.

placement of the peg. This effect was tested in two ways: (1) by growing seeds upon a clinostat with coats intact and with coats removed at tips, and (2) by a similar growth of seeds held between cork strips with radicles pointing downward or approximately so. These were kept in a dark chamber and watered with a spray at 23° C., as described above. There is some variation in different varieties in the response to contact. For example, the pump-

kin called Big Tom, especially when grown on the clinostat, gives a somewhat higher percentage of strong arching in response to coat contact than does the Hubbard squash. Fig. 2 shows all the individuals of a culture of Hubbard squash grown as described above, coats removed at tip, and radicles pointing downward. Of the 26 seedlings, none are sharply arched, and all have pegs either two-sided or ringlike. Three show slightly more prominent pegs on one side than on the other. It is evident then that in

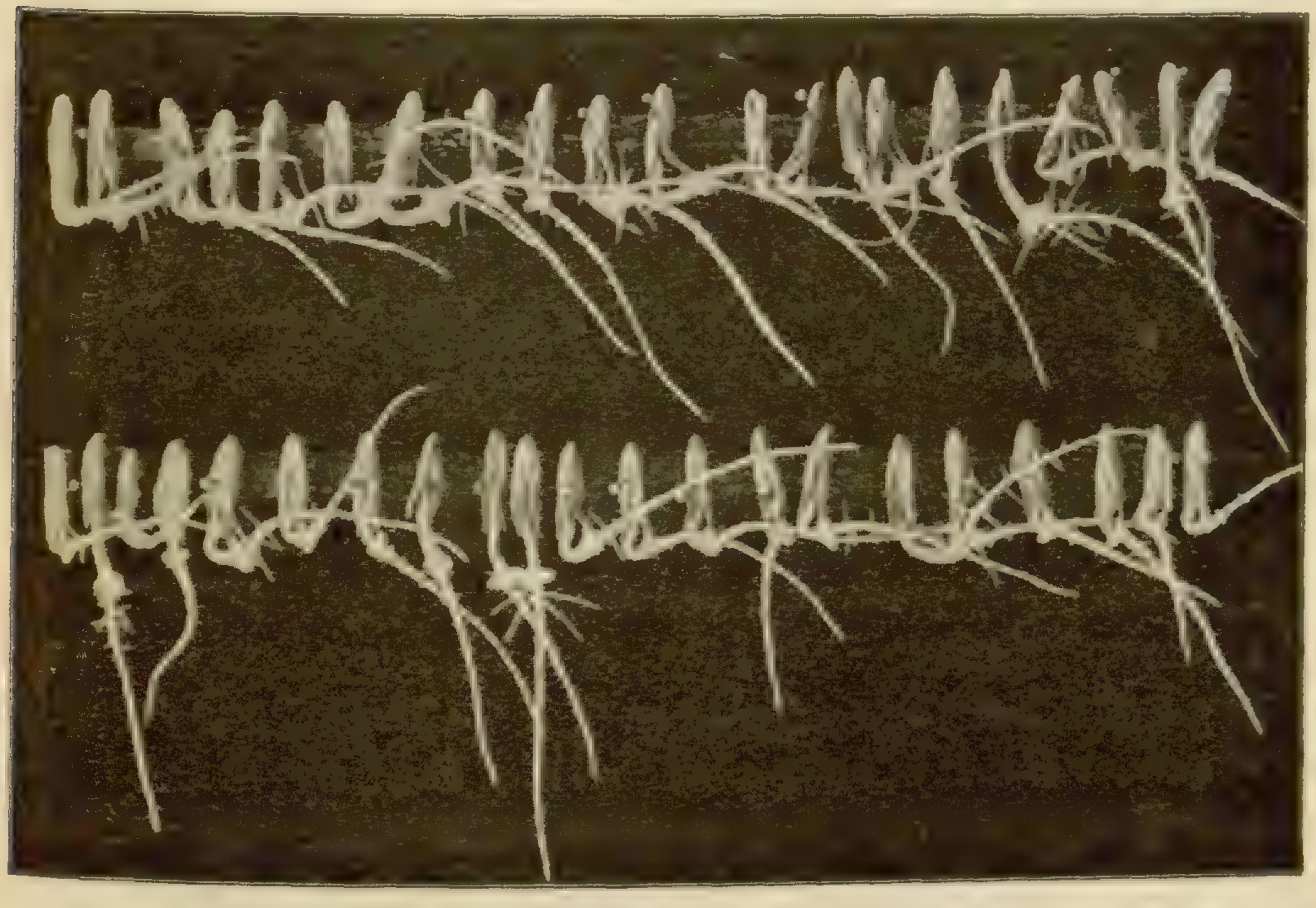

FIG. 3.—Crop of Hubbard squash as in fig. 2, but coats not removed at tip; shows sharp arching induced by contact of coats.

the Hubbard squash little arching and no one-sided pegs are produced if the seedlings grow with the radicles pointing vertically downward, and with no contact of either coat or media. Fig. 3 shows a similar culture except that the coats were intact during the growth. Of the 42 seedlings, 29 are sharply arched and 13 very slightly or not at all. This shows contact of coats to be very potent in arch-production. Of those that are sharply arched, 8 have pegs entirely on the concave side of the arch, while several others show the greater peg-development on that side. In this case the arching is against gravity, which emphasizes the potency of con-

tact of coats as a stimulus to arching. By a comparison of figs. 2 and 3, one can see clearly the effect of contact upon the size of the peg.

A culture of pumpkin (Big Tom), with coats removed, radicles pointing vertically downward, and grown in a spray as described above, produced 39 seedlings. Of these none were sharply arched; 19 showed very small two-sided pegs; 19 were essentially pegless; and 1 showed a small one-sided peg on the concave side of the slight arch. A similar culture of the pumpkin (Big Tom) with coats intact gave 31 seedlings; of these, 25 were sharply arched, with pegs entirely on the concave side of the arch; 1 was little arched, with peg on concave side of arch; 3 were pegless; and 2 had equal, small, two-sided pegs. From these data it is evident that in the pumpkin (Big Tom) contact of coats is even more effective in producing arching than in the squash (Hubbard), and unlike the case of the squash, the arching shifts the peg entirely to the concave side of the arch. From the large number of pegless seedlings appearing in the culture with the coats removed, it is also evident that the arch not only determines the lateral placement of the peg, but in some cases even its appearance. One may be inclined to think the existence of the peg is perhaps determined by the contact of the coat, rather than by the arching produced by the coat; but it is not probable, for of the 6 not arched in the culture with coats on, 3 are pegless. It is apparent, therefore, that a large number of the pumpkins (Big Tom) are pegless if developed without considerable arching, and that arching determines in about half the cases whether or not there will be a peg, as well as the placement of the peg on the concave side of the arch.

Fig. 4 shows a culture of pumpkin (Big Tom) with coats removed at the tips, and grown on the horizontal clinostat in a spray. Of the 30 seedlings in the culture, none are sharply arched; 14 have small two-sided pegs; 8 show slight pegs on the concave side of the slight arch; and 8 are essentially pegless. Fig. 5 shows a similar culture except the coats are intact. Of the 24 seedlings, 20 are sharply arched, with pegs entirely on the concave side of the arch; 2 are slightly arched, one of which has an equal two-sided peg and the other a slight one on the concave side of the arch;

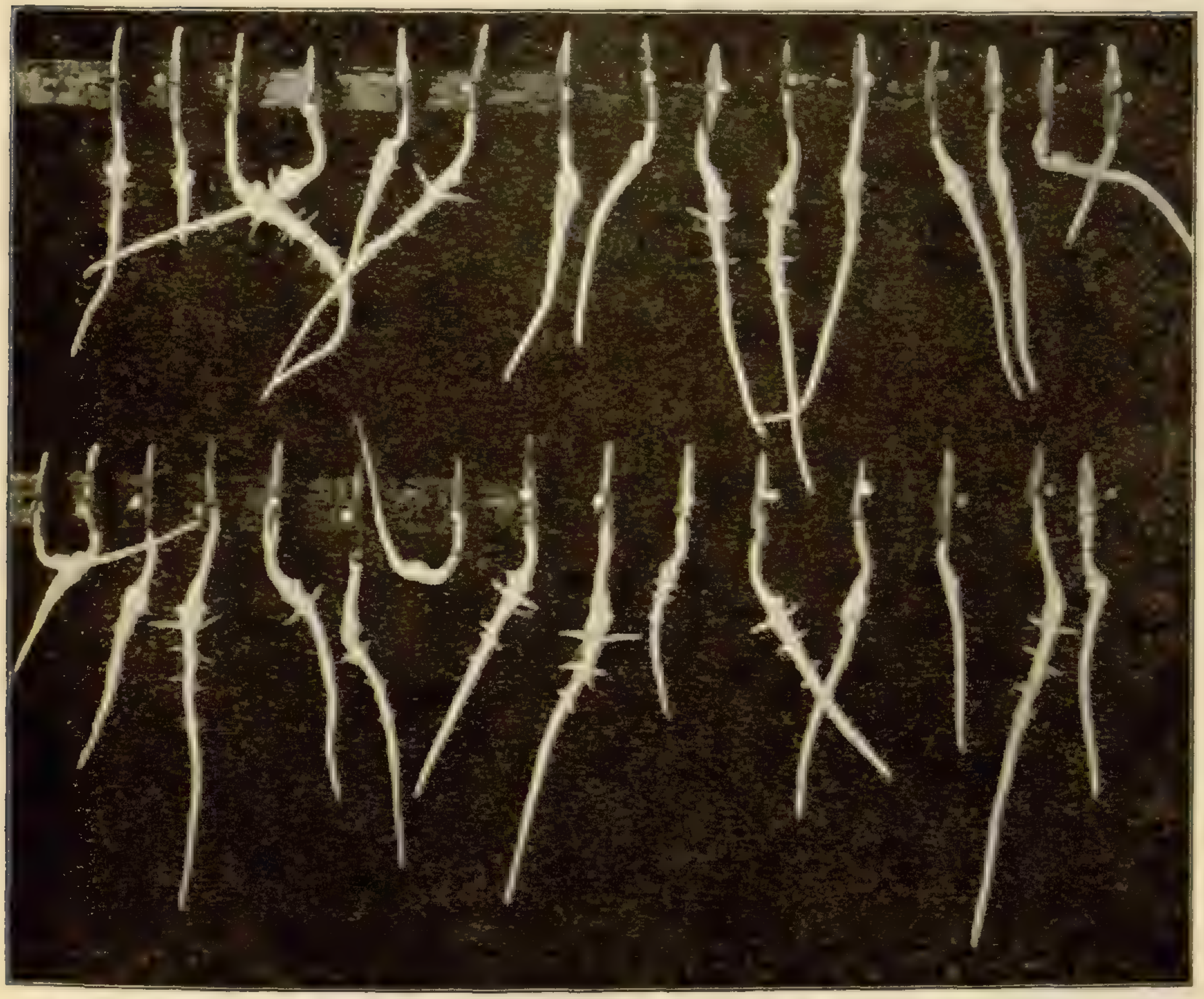

FIG. 4.—Crop of Big Tom grown on a clinostat in a spray; temp. 23°; coats removed at the tip.

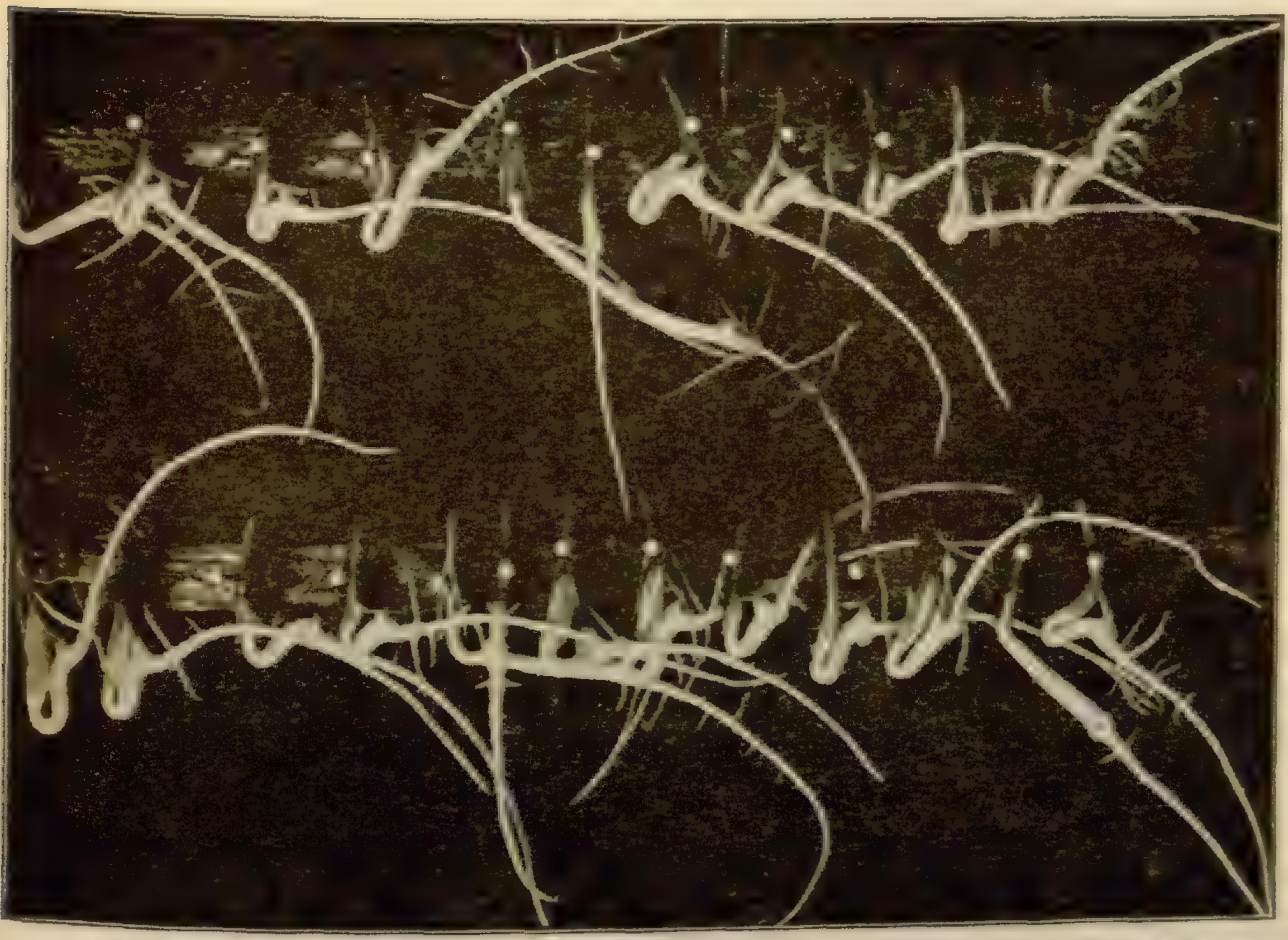

FIG. 5.—Crop of Big Tom grown as fig. 4, except coats were not removed at the tip.

2 show no arch and are essentially pegless. One is struck here by the small percentage of pegless seedlings in the culture in which the coats are removed, as compared with corresponding seedlings grown with the radicle pointing vertically downward. This is easily explained, however; the arching does not have to take place against gravity, due to the equalization of this stimulus by the clinostat. In short, the autonomic disposition to arch is unrestrained. This fact, with the fact that slight arching produces a one-sided peg in this form, makes the data exactly what must be expected. Again, one sees that the contact of the coats is much more effective in producing arching and one-sided peg-development than in the culture in which the seedlings developed with the radicle pointing vertically downward. This again must be expected, for the arching does not have to occur in opposition to gravity, since this stimulus is equalized by the clinostat.

NOLL states that more than 50 per cent of pumpkins grown on a horizontal clinostat show sharp arching, with the peg entirely on the concave side of the arch. This is the case if one allows two factors to act at once: contact of coats and the autonomic tendency to arch. But NOLL'S conclusion that such results will follow from the autonomic tendency to arch alone is erroneous, and was possible only because he overlooked the very important influence of contact of coats in the arching. DARWIN'S statement that in seedlings of *Cucurbita ovifera*, grown on the clinostat, the peg is almost equal on all sides, certainly holds for the squash (Hubbard), providing both contact of coats and media are avoided, as they were in our clinostat cultures.

From the experiments stated in this section several things are evident. Contact of coats is an extremely important stimulus for arch-production, both in the pumpkin and the squash. It produces strong arching even against gravity. In the pumpkin (Big Tom) any considerable arching increases greatly the percentage of seedlings that show pegs; and it causes the development of the peg on the concave side of the arch. In the squash (Hubbard) arching is far less effective in determining the lateral placement of the peg. The autonomic tendency to arch is very slight, though it tends to a lateral placement of the peg in the pumpkin (Big

Tom), as shown by the clinostat experiments where the coats are removed. It is also evident that results obtained without reference to the effect of contact of the coats cannot lead to a knowledge of the part played by the several factors in determining the lateral placement of the peg.

EFFECT OF DEVIATION FROM THE VERTICAL POSITION

As has been stated, NOLL claimed that seedlings grown in a vertical position, with the radicle pointing downward, gave two-sided or ringlike pegs. He found, however, that a slight deviation from this position (8°.5) produced only one-sided pegs. We ran numerous experiments on various varieties of cucurbits for the purpose of testing this statement. The results are tabulated in the accompanying table. "Vertical" in this table means that the seed was held so that the plane passing through the largest dimension of the seed was in a vertical position and the radicle was pointing downward. Deviations from this plane were made by tilting the plane of the seed the number of degrees from this position that is recorded in the table. The tilting always exposes one face rather than the edge of the seed to gravity. The seeds were held in position by two pieces of cork lightly clasping them at the central region. The whole culture was grown in darkness in a spray, so that no contact of media was involved and no contact of coats except when specified.

A glance at this table makes it very evident that it furnishes no ground for NOLL's conclusion that a deviation of over 8°.5 gives only one-sided pegs. Our extensive experiments make us unable to understand how he obtained such results.

It is evident from the table that in every variety used the deviation from the vertical is far more effective in the lateral placement of the peg when the coats are intact than when they are removed at the tip. This is due to the fact that the arching is made much sharper by the coat contact, and the lateral placement is in turn furthered by the sharper arching.

It is also noticeable that there is a great variation in the several varieties in the effectiveness of the deviation for the lateral placement of the peg. In Big Tom it is most effective, while in Boston

Deviation from vertical position		Vertical			10°			20°			30°			45°			65°			90°			135°			150°			165°			180°		
Nature of peg		1-sided	2-sided	pegless	1-sided	2-sided	pegless	1-sided	2-sided	pegless	1-sided	2-sided	pegless	1-sided	2-sided	pegless	1-sided	2-sided	pegless	1-sided	2-sided	pegless	1-sided	2-sided	pegless	1-sided	2-sided	pegless	1-sided	2-sided	pegless	1-sided	2-sided	pegless
Variety	Condition of coat at tip																																	
Big Tom (pumpkin)	removed	6	27	37	0	4	5	1	6	6	0	11	4	16	27	5	18	6	0	47	19	0	59	0	0	60	0	..	57	0	..	42	0	..
	intact	30	7	1	15	1	0	16	4	1	3	3	..	35	4	0	17	0	0	43	1	0	101	0	1	30	0	..	46	0	..	50	0	..
Hubbard (squash)	removed	5	44	1	0	8	0	3	10	..	..	..	..	22	41	0	..	..	..	38	3	0	38	3	0	..	..	..	..	..	..	..	..	..
	intact	3	23	1	1	10	0	1	12	..	..	..	..	27	17	0	..	..	..	46	2	0	46	2	0	..	..	..	..	..	..	..	..	..
Boston marrow (squash)	removed	..	..	..	..	..	..	22	22	..	1	27	..	0	6	0	5	15	..	..	..	..	19	9	0	24	8	0	54	3	0	58	4	..
	intact	..	..	..	6	29	..	6	42	..	13	11	..	..	..	..	8	4	..	..	..	..	35	2	0	38	5	0	47	4	0	45	1	..
Calhoun (squash)	removed	..	..	..	..	..	..	..	..	..	0	23	..	2	13	0	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	intact	..	..	..	..	..	..	..	..	..	2	13	..	4	5	0	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Sugar pie (pumpkin)	removed	..	..	..	..	..	..	..	..	..	8	2	7	27	31	4	..	..	..	103	29	12	..	..	..	..	..	..	..	..	..	..	..	..
	intact	..	..	..	..	..	..	..	..	..	9	3	9	23	4	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..

marrow it is least so. In the former no two-sided pegs appear at 135° deviation or above, while the latter at 180° deviation still shows about 8 per cent with two-sided pegs.

In the exposures with the coats removed, one can see the effectiveness of gravity alone in the one-sided peg-production. It must not be forgotten that the effect of gravity in lateral placement of the peg is probably entirely indirect and acts through the production of an arch.

As has been mentioned, NOLL thought that not only the development of the peg but its lateral placement is called forth by the joint action of two heterogeneous stimuli: gravity, which causes the development on the lower side of the hypocotyl; and "organform" stimulus, which causes the development on the concave side of the arch. NOLL compared the second of these to the appearance of lateral roots on the convex side of a curved main root. His main evidence for the conclusion concerning two heterogeneous stimuli is based on his experiments in which he grew seedlings at various deviations from the vertical (radicles pointing downward). If his statement that any deviation beyond 8°.5 always produces a one-sided peg were true, his conclusion would be entirely justified. Our results, derived by the use of five different varieties of cucurbits, of very different characters so far as peg-development is concerned, and obtained with greatest care in eliminating all factors, except gravity, show that it takes a deviation of not merely 8°.5, but in every case of more than 90°, and in forms like the Boston marrow of more than 135°, to insure a one-sided peg. When a seedling grows in the horizontal position, gravity and the "organform" stimulus certainly are both acting to produce the peg on the lower side only, and yet our results show that many seedlings thus grown produce two-sided pegs. NOLL's two heterogeneous stimuli are not adequate to explain these results. This view becomes yet less in accord with fact when it is remembered that NOLL assumed that gravity could not reach more than 8°.5 over the lower pole of the hypocotyl, that is, that gravity is not effective in inducing peg-development on the upper side of the hypocotyl if the deviation from the vertical is over 8°.5.

It has already been pointed out that in *Eucalyptus* and *Cuphea*

a ringlike peg is laid down in the formation of the seed, and with germination this enlarges somewhat. In these forms, therefore, the peg is a natural outgrowth approximately equal on all flanks of the seeds; its appearance and development are related, undoubtedly, to the plant form and not called forth alone by external stimuli. We find that such a ringlike peg, rather small but approximately equal on all flanks, develops on the seedling of palo verde (green-stemmed *Parkinsonia*). In this form the arching of the hypocotyl is not marked and the peg does not function in the removal of the coat; likewise, external conditions do not seem to lead to a lateral placement. Results already stated, as well as data to be stated later, lead us to believe that the peg of the cucurbits is, to a considerable degree, a natural outgrowth of the seedling, and that it is approximately equal on all flanks if arching is avoided. We must of course accept the quantitative greater development on the two broader faces of the hypocotyl over the two narrower. It is also evident that in different species the size of the outgrowth varies greatly; it is relatively large in squashes (Hubbard, Boston marrow, and Calhoun), and relatively small or even absent in pumpkins (Big Tom and Sugar pie). We have also found the latter to be the case in various watermelons and cucumbers. In fact, if arching is avoided, different species will show all the intermediate forms from the so-called pegless (fig. 6) to those that have very prominent ringlike pegs. We must also recognize that the contact of coats, as figs. 2 and 3 show, greatly increases the size of this outgrowth. The size is also greatly increased, at least on one flank, by arching.

FIG. 6.—Pegless seedlings of Big Tom.

The question, therefore, does not seem to be so much what stimuli cause the development of this organ, as DARWIN and NOLL assumed, but rather what stimuli lead to its lateral placement and tend to increase its size.

It is certainly evident, as all who have worked on this subject agree, that arching or "organ-form" stimulus, as NOLL termed it, leads to the shifting of the peg to the concave side of the hypocotyl, or, as it would be better termed, to the development of the peg on the concave flank of the hypocotyl. Both gravity and contact of coats aid in arch-production. Of these, as our results show, the latter is much more important. Contact of coats also greatly increases the size of the peg. Other questions that should be answered in this connection are whether or not gravity acts as a direct stimulus in the lateral placement of the peg, and whether or not it tends to increase the size of the peg on the flank exposed to it.

As has been repeatedly said, both DARWIN and NOLL assumed that gravity is a direct stimulus, not only in determining the existence of a peg but also its lateral placement. DARWIN'S evidence for this was that a ringlike peg is found when the seedlings of *Cucurbita ovifera* were grown in a horizontal position on a slowly rotating clinostat. NOLL'S evidence for this conclusion included two other facts: (1) seedlings with the radicle pointing downward but deviated more than 8°.5 from the vertical gave pegs only on the lower side, and (2) seedlings turned over every few hours during development gave pegs ringlike or two-sided. We have shown that NOLL'S deviation experiments do not at all accord with results obtained with all care to avoid the variation of more than one factor at a time. As for the clinostat and turning evidence, it is just what would be expected if the peg is an outgrowth approximately equal on all sides, if sharp arching is avoided. Of course the clinostat and the turning from time to time prevent sharp arching, and thereby give the natural ringlike or two-sided development.

Further evidence as to whether gravity is a direct stimulus in determining the existence of a peg, its lateral placement, or its size, is found in the sections that follow.

CENTRIFUGE CULTURES

A large number of cultures of the several varieties of cucurbits worked with were made on a centrifuge with a vertical axis. The acceleration varied from two gravities to eighteen gravities. The

cultures were grown in a spray at 23° C.; the coats were removed to avoid all contact; and the long axis of each seed was arranged parallel with a radius of the centrifuge, the radicle directed away from the axis.

Three facts were noticeable in such seedlings, especially in those grown with the greater centrifugal acceleration: (1) the hypocotyls were very straight, (2) the pegs were smaller than in similar cultures on clinostat or with radicles pointing vertically downward, and (3) the pegs though small were approximately equal on all flanks.

If, as NOLL assumes, gravity calls forth the peg in seedlings with the radicles pointing downward, one would expect larger pegs with increased gravities, unless the rather remarkable situation exists that one gravity is the optimum or is greater than the optimum for peg-development. But how can one account for the more meager and very regular peg? This is undoubtedly due to all arch strains being overcome by the centrifuge, which removed this stimulus to the enlargement and unequal distribution of the peg.

It must not be forgotten that a centrifuge thus operated gives two mass accelerations at right angles to each other: one due to the centrifugal acceleration produced by the machine and acting in the direction of the pointing root, and one gravity downward. If a flat side of the seedling faces downward, and the machine gives a centrifugal acceleration of three gravities, three gravities act in the direction of the pointing root and one gravity downward. Such cultures showed very slight tendency to arch, and no greater peg-development on the lower than on the upper flank. If this organ were sensitive to gravity, one would expect it to show a greater response on the side where one extra gravity was acting, especially when the centrifugal acceleration was only three gravities. Of course it is entirely possible that WEBER'S law applies in such proportions that the application of one gravity as a stimulus cannot be perceived when three gravities are acting at right angles to it. In geotropism of *Vicia Faba* epicotyls, however, WEBER'S law applies in the proportion of 24–25, that is 4 per cent excess exposure to gravity in one direction is sufficient to give a response.

It must be remembered that while this experiment does not prove that gravity is not a direct stimulus in determining the size and lateral placement of the peg, it certainly furnishes no evidence that it is.

A detailed statement of the results of one experiment with Big Tom on a centrifuge with a horizontal axis will suffice to indicate the nature of the results obtained with that apparatus. Here, also, the coats were removed at the tip and the temperature kept at 23° C. by means of a spray. The revolutions were 440 per minute and the circles 3 and 6 inches in diameter. The 3-inch circle gives 8.25 gravities, while the 6-inch gives 16.5. In the 3-inch circle 15 were essentially pegless and 2 with slight two-sided pegs. In the 6-inch circle 25 were essentially pegless, 4 with slight two-sided pegs, and one with a peg toward one edge of the seed. The marked tendency to show pegless forms is manifested here, as in all experiments on the centrifuge, with three or more gravities. It seems that these accelerations prevent all disposition to arching and to arching nutations; hence they give many pegless forms.

OBLIQUE CLINOSTAT CULTURES

A number of cultures were made on the oblique clinostat as devised by FITTING.[10] The cultures were watered by a spray at 23° C. and grown with coats removed at the tip to avoid contact. The end of the clinostat axis to which the frame for bearing the seeds was attached was pointed upward from the horizontal, while the radicles of the seeds pointed toward the axis. This insures, as an understanding of the oblique clinostat will show, that extreme arching is avoided. The axis was placed at various angles with the horizontal, and the large plane of the seeds at corresponding angles with the axis. When the axis varied 5° from the horizontal, and the large plane of the seed was broken 5° from the axis, at one point in each revolution one flat face of the seed was exposed to gravity at an angle of 80° from the vertical (radicle pointing downward) and the other face at 90°. As soon as considerable growth occurs, of course geotropic response occurs in favor of the 90° exposure, and this throws the flank of 80° exposure more nearly

[10] See footnote 7.

90°, thereby avoiding sharp arching. The difference of exposure is marked then only in the early stages, and other exposures with 90° against 76° and 90° against 85° gave no peg-development in favor of the 90° either in the pumpkin or squash. It has been shown that the effectiveness of geotropic stimulus in orthotropic organs is approximately proportional to the sine of the angle, and therefore the 90° exposure is stronger than any of the others. If gravity is effective as a form stimulus in causing the lateral placement of the peg, we might expect it to be manifested by a larger peg-development on the flank exposed at 90°. These experiments give no indication of it, and yet it would hardly be expected that such differences in exposure would show an effect, since much greater differences failed to do so in the centrifuge experiments described above. It must also be pointed out that, unlike the centrifuge experiments, these experiments are rather unsatisfactory because the arching occurs in favor of the 90°, and that factor is sufficient, if great, to produce lateral placement of the peg. On this account, only angles differing rather slightly can be compared. It is evident, however, that these experiments, as do the centrifuge experiments, furnish no evidence that gravity is a direct stimulus to the lateral placement of the peg.

General and summary

As one sees from the experiments given above, there is *no evidence that gravity acts as a direct stimulus to the lateral placement of the peg*. Certainly, then, DARWIN is not justified in using this assumption as a main prop to a theory (mnemic theory) which itself looks away from rather than toward progress in the knowledge of plant response.

Assuming that all arching is avoided, the following facts seem to hold: the peg is to a considerable degree a natural integral part of the plant; it develops on all flanks of the hypocotyl approximately equal (granting perhaps that it is somewhat larger on the broad flanks in many of the cucurbits); it varies in size from the very slightest outgrowth appearing in a small percentage of Big Tom to the large pegs of the Hubbard squash.

It may be laid down with the formation of the seed, as in

Eucalyptus and *Cuphea*, where it is an equal ring all around the organ; or its formation may begin after germination, when its position and size are determined by the factors we have shown to be effective.

The lateral placement is apparently brought about by the arching of the hypocotyl. Two stimuli aid in the formation of the arch: contact of the coats and gravity. Contact of the coats is by far the more effective, for it will induce very sharp arching even against gravity.

In forms like the Boston marrow, gravity independent of contact with a deviation of 170° from the vertical gives strong enough arching to produce only 90 per cent with one-sided pegs. In Big Tom and various other forms it is somewhat more effective.

Arching leads to an increased development of the peg, as well as to its lateral placement, and in many cases it produces a peg where it would not otherwise appear, as in Big Tom. Contact likewise increases the size of the peg independent of its effect through arch-production.

No evidence obtained from this detailed study indicates that gravity, as a direct stimulus, in the least increases the peg-development.

THE UNIVERSITY OF CHICAGO

THE ORIGIN AND DEVELOPMENT OF BULBS IN THE GENUS ERYTHRONIUM[1]

FREDERICK H. BLODGETT

(WITH PLATES VIII–X AND SEVEN FIGURES)

Introduction

The genus *Erythronium* includes some fifteen species of bulbous plants of the north temperate zone, one of which occurs from the Pyrenees, across France, southern Europe, and Asia, to Korea and Japan. The remaining species are North American.

The plants are perennial through the annually renewed bulbs. These are developed at gradually increasing depths from the seedling to the flowering stage, after which they are formed at a nearly constant depth in the soil. The bulb consists of a few thick scales surrounding the stem apex; the aerial structures push upward from the base through the cavity inclosed by the inner scale. The first aerial structures are single leaves, two leaves and flowers appearing only after several years.

Special details of the development of one or another of the species have been examined by several writers; but some stages have been omitted in these accounts, and in others some obscurity exists as to the exact nature of the structures mentioned. A consecutive account of the development of the plant, with special reference to the origin and structure of the stem apex, and its outgrowths, from its inception in the embryo to the final formation of the flower bud, is the subject of this paper; which is thus a study of the vegetative development of the sporophyte, consideration of the gametophyte being omitted.

Erythronium americanum is taken as the basis of the study, since material of this species is abundant in the vicinity of Baltimore, and especially since it shows more specialization in its vegetative development than do the other forms. Comparisons have been made with other species, as will be noted, and the

[1] Contribution from the Botanical Laboratory of the Johns Hopkins University, no. 14.

differences found have a probable bearing upon the evolution of the genus.

Material was killed in chromacetic acid, and cut usually 10 μ in thickness; except in the case of the hard seeds, no special methods were necessary.

To Professor DUNCAN S. JOHNSON the author wishes to express his thanks for helpful criticism and maintained interest during the progress of the work.

Germination

The flowers of *Erythronium americanum* appear during the first week of April in this region, and the seeds ripen early in June, from which seedlings arise the following March. The main body of the seed measures about 4×2 mm., but a spongy spur at the chalaza and a fleshy raphe nearly double the bulk of the seed, subject to individual variation. The embryo in the ripe seed is slightly pointed toward the micropyle, but is otherwise undifferentiated (fig. 1).

Germination begins about the middle of September, when the seed becomes moistened by the fall rains, and the embryo begins to elongate. The growing embryo enlarges first to occupy the space filled by the spongy endosperm, in which it is imbedded, ordinarily by the first week of October. The tip of the cotyledon is organized into a haustorial organ, by which the hard endosperm is absorbed. Elongation proceeds slowly during the fall, so that the embryo is half the length of the seed in December (fig. 2). The rate of growth seems to be closely related to the abundance of moisture in the soil. The tip of the radicle is pushed about the end of the year through the micropyle. The stem apex at this stage appears in a narrow cavity extending from the surface nearly to the center of the tissue just behind the radicle. The hypocotyl does not elongate, and is practically absent. As the embryo continues to elongate, the stem apex is carried forward, and retains a constant position in relation to the radicle during the elongation of the cotyledon (fig. 3). The zone of elongation during this time is in the lower part of the cotyledon, just above the cavity in which the stem apex is situated. Growth is nearly vertical, and after penetrating the soil 1–3 cm. the descending axis comes to rest.

When the endosperm has been exhausted, the elongation of the descending axis ceases. The zone of elongation in the cotyledon is now located near the upper end of the cotyledon, so that the tip of the cotyledon is withdrawn from the empty testa, and elevated into the light, much as in *Allium* (SACHS 18). From the haustorial cells at the tip of the cotyledon two vascular bundles extend downward to the base of the root, just below the level of the stem apex, as in *Tulipa* (IRMISCH 11). In some species (*E. grandiflorum*, and *E. Hartwegii*) there are three cotyledonary bundles (SARGANT 19). After reaching the light, the cotyledon attains a total length of 8–10 cm. above the soil line (text fig. 6), and the elbow formed in the withdrawal from the seed coats gradually straightens. The cotyledon is cylindrical below, but may be considerably flattened in the upper portions, the two bundles lying side by side (figs. 4, 5).

The apical dome becomes differentiated during the descent of the stem apex, and the cavity in which it is inclosed changes into a curved pocket by the elongation of the walls of the cavity (figs. 6–10). The apex then rises as a dome from the bottom of the pocket. The space about the apex has a depth about equal to its width when the descending axis comes to rest. The thickness of the walls decreases from the axial to the opposite side, which lies immediately below the opening from the interior of the cavity to the exterior. The base of the cotyledon thus comes to form a sheath about the stem apex. The radicle has as yet grown but little; soon, however, the primary root is organized and advances from the end of the descending axis (text fig. 1). The primary root is the only one in the life cycle which responds positively to gravitation. At the base of the root a considerable cushion is formed, upon which root hairs are produced abundantly. By the growth of adjacent tissues the base of the root becomes oblique, and seems to be fused to the side of the cotyledonary sheath for a short distance (figs. 6–9). The stem apex, or plumule, has so far no vascular supply from the rest of the seedling, the cells below the apical dome being meristematic and undifferentiated as yet into tissues. The plumular trace is inserted upon each of the two cotyledonary bundles, just before they unite to form the root

stele, the region of fusion being about 0.5 mm. in length (figs. 16–20). This theoretically constitutes the "hypocotyl" in these seedlings (SARGANT 19).

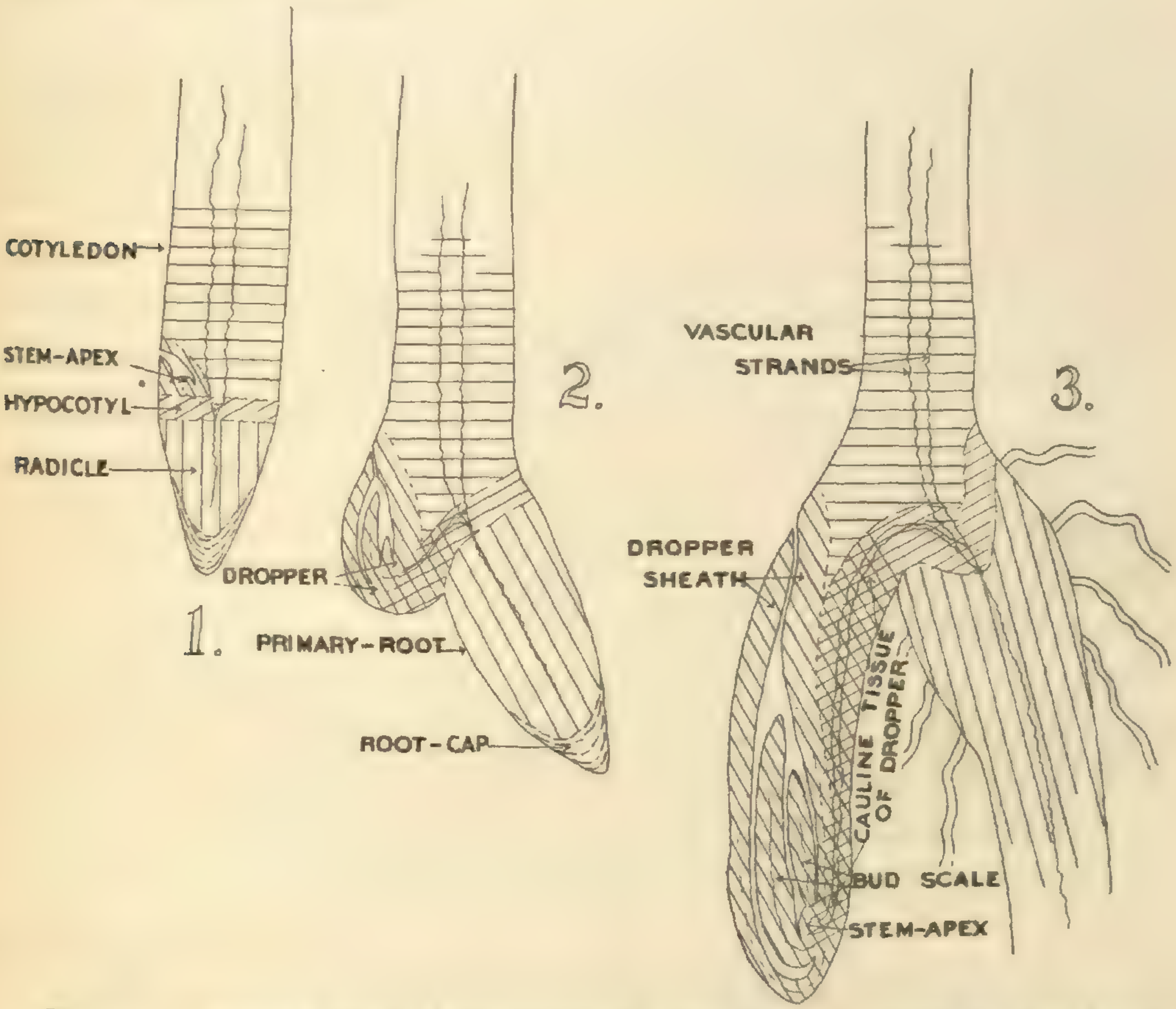

FIG. 1.—Diagram showing development of seedlings: *1*, descending axis during first stage; *2*, inception of droppers and development of root; *3*, dropper actively elongating downward, second stage of descent.

First vegetative period

The cotyledon functions as the first foliage leaf, and provides material for the further descent of the stem apex. Abundant stomata and large intercellular spaces are present in the body of the cotyledon; moreover it has the power of recovery from wilting to a high degree. This was found by allowing the soil to become dry and then watering, when seedlings which had become prostrate recovered their erect position, unless the cells had actually been killed. The cells nearest the tip were the first to show the effects of too great drying.

Soon after the cotyledon becomes active photosynthetically,

and the primary root is protruded into the soil from the end of the descending axis, the further descent of the stem apex begins. The sheath in the base of the cotyledon, in which the apical dome is located, elongates by the proliferation of the cells in the walls of the sheath so that the base of the cavity is lowered in reference to other points. As the structure so formed is positively geotropic in its growth response, it may conveniently be called a "dropper." The apical dome, being inserted at the base of the sheath, is carried forward in the elongation as a terminal bud (figs. 10, 13).

The dropper originates from the cotyledonary sheath through the irregular distribution of the dividing cells in the walls of the sheath. The base of the sheath is displaced laterally by the multiplication of cells between the apical dome and the axis of the cotyledon (figs. 6–8). This pushes the base outward from its original position. While the displacement is proceeding in the lateral direction, an elongation is also taking place, so that the dropper begins to push forward into the soil during its displacement. Soon after the axis of the dropper becomes established as a direction of growth, the zone of elongation becomes confined to the region immediately adjacent to the base of the apical dome. This places the growing tissue close to the apex of the dropper, as if it were a rhizome.

The inclosing walls of the dropper do not grow equally, the axial wall elongating more slowly at first than the abaxial, resulting in a lagging behind of the apical dome, in reference to the base of the sheath cavity. The stem apex thus becomes located on the side wall, instead of at the base of the sheath (fig. 13). The axis of the dome itself may become almost horizontal through this displacement. The oblique position of parts inaugurated at this stage of development persists through the life cycle, including the deep-seated bulbs of the flowering individuals. The lateral location of the stem apex at the base of the sheath cavity causes a distortion of the outgrowths from the apical dome as they appear. The apical outgrowths push upward into the cavity about the stem apex, and thereby appear to be at nearly right angles to the axis of the dome (fig. 13). The rate of growth of the apical dome and that of the developing scale is so nearly identical that the dome

itself is lost as a distinct group of cells. When the scale has so far developed that the margins of the leaf rudiment meet in front of the median line of the scale, then the apical dome becomes distinguishable again. The dome then forms a low mass of cells projecting from the face of the axial side of the scale into the space inclosed by the united margins. Continued growth soon makes the dome more conspicuous, and at the same time readjusts its position to a more central point (figs. 10, 12, 13). The tissues of the scale rudiment and of the stem apex are nearly alike in their staining qualities, and continue to be meristematic until a considerable size is reached. Thus in the first stages of scale formation, the growth in length of the apical dome and the growth in thickness of the scale rudiment are so nearly equal that there is no difference in staining reaction to aid in separating the two morphologically different tissues. It is not until the scale leaf has inclosed the apical dome by the forward growth of the margins of the scale, that the dome is to be separately recognized. This obscuring of the apical dome appears to be a recurring feature in the normal development of the bulbs, as the successive bulb scales are formed.

The dropper grows downward to a distance varying from a few millimeters to 4 (rarely 5) cm.; in most cases the dropper is about 2.5 cm. in length. This growth is accomplished during the period of activity of the cotyledon as a leaf, by which the needed starch and other materials are elaborated. At the end of three or four weeks of development, the apical bud within the dropper sheath becomes enlarged by the deposit of storage starch, and the stem apex with its inclosing bulb scale becomes the primary bulb (fig. 14). The seedling dies from the apex of the cotyledon backward, gradually involving all tissues except the bulb, which thus becomes isolated in the soil. The withered walls of the dropper sheath form a husk about the bulb. In the axil of the dropper sheath a bud is formed, which rarely develops.

During the active descent of the dropper, vascular connection from the stem apex to the base of the cotyledon is maintained through the bundles in the axial wall of the dropper. This tissue is to be regarded as cauline in character, since it terminates in the growing point of the stem. In its earliest stages the vascular

strand appears as a few elongated cells between the base of the apical dome and the base of the cotyledonary bundles (figs. 8–10, 16–20); as the dropper elongates these cells increase in number by additions at the growing end, and become more completely differentiated into vascular elements (figs. 8, 11, 13). At the end of the strand branches are given off into the scales developed from the apex. The vascular elements are only slightly developed in the bulb bundles, since there is little strength required, and the bundles are surrounded by abundant parenchyma. The spiral vessels are the most easily distinguished parts of the bundles.

During the summer the bulb shows no external signs of activity, but the stem apex is then organizing the first foliage leaf for the second vegetative season. In its inception the leaf resembles a scale leaf, but soon becomes differentiated into a blade and a basal portion. By the elongation of the base, the blade is elevated above the stem apex (fig. 15, *l*). The apical dome is thus left in a position simulating that of an axillary bud, with the leaf as its subtending organ. But the further development of the dome, as well as its immediately preceding history, identifies this as the stem apex. The leaf and the apical dome are in the relative development given about July 1.

In the development of the foliage leaf, the elongation of the petiole lifts the lamina above the stem apex before the latter becomes inclosed by the development of the margins of the blade. The margins grow outward from the median portion of the leaf rudiment, their edges passing each other above the level of the stem apex. The base of the petiole grows about the stem apex, so that this becomes inclosed in a sheath much as was the apical dome in the cotyledonary sheath. A small opening connects the cavity of the sheath with the space outside the petiole in the bulb.

At this time there appears in the axil of the leaf an axillary bud, which from its position in reference to the apical dome seems to be borne upon the surface of the dome, rather than to be truly axillary to the leaf. A bud is also developed in the axil of the inclosing scale. The stem apex develops usually two bulb scales during the late summer, thus forming a bulb rudiment at the base of the leaf by the close of the year. In these primary bulbs the stem

apex alone develops into a bulb in most cases; but in older plants the axillary buds may also develop into bulbs. When the bulbs of any age are renewed *in situ*, the apical bud forms the single new bulb; but when there are runners developed, the axillary buds also form bulbs, being then the terminal buds of runners which become isolated in the soil as in the case of the primary bulb from the dropper.

Second vegetative period

The second vegetative period in the life cycle of the individual begins in September, when the roots protrude from the base of the primary bulb. These are few in number, three in most cases, and do not respond positively to gravitation. The root rudiments originate just below the region where the vascular strands from the dropper give off branches into the stem apex and the bulb scales. These stages are shown at *r* in figs. 24, 26, 27. The roots grow nearly straight from the point of origin to their limit of growth. They maintain a spatial relation toward each other so as to be equidistant in the soil. The oblique position of the base of the bulb makes the cluster of roots which radiate from the base appear lateral (JOST **14**, p. 27) at the lower end of the bulb. In the older bulbs the roots are more numerous, and their lateral insertion is but slightly changed. The position of the roots in the soil is such as to define a nearly flat cone, with its axis in line with the axis of the apical dome. The angle taken by the axis of the cone varies slightly as the obliquity of the individual bulb differs, but lies close to 45° to the vertical. Under experimental tests, different positions of the bulbs used did not change the position of the axis of the cone of roots in reference to the axis of the apical dome, although the latter was itself placed in abnormal positions in respect to the vertical. Roots are rarely found within the conical mass of soil outlined by most of the roots; when so found, the roots are very numerous and some are crowded away from the peripheral portion of the meristem cells in the base of the bulb.

During their growth from the point of their inception to the surface of the bulb, the root rudiments pass through the tissues at the base of the bulb, a thickness of 1–3 mm. according to the size of the bulb. In passing through the bulb the advancing tip of

the root rudiment appears to come into contact with the cell walls at intervals only. This is indicated in sections by the presence of a cavity about the root tip, the bulb parenchyma being separated from the root itself by a space in which there appear no cell walls. In the cells at a little distance from the line of advance of the root, scattered starch grains appear, and the normal starch content remains in the bulb parenchyma farther from the root cluster (text fig. 2). It appears that the starch is first removed from the cells in the path of the advancing root rudiments, then as the root is organized and grows forward, the cells themselves are disintegrated, leaving a clear pocket immediately about the conical end of the root. Only at the sides of these cavities were there any flattened cells, as if contact had occurred between the root tissue and the surrounding parenchyma. But as the root issues from the base into the soil, there is a collar of cells about the base, which constricts the root at this point to a slight degree.

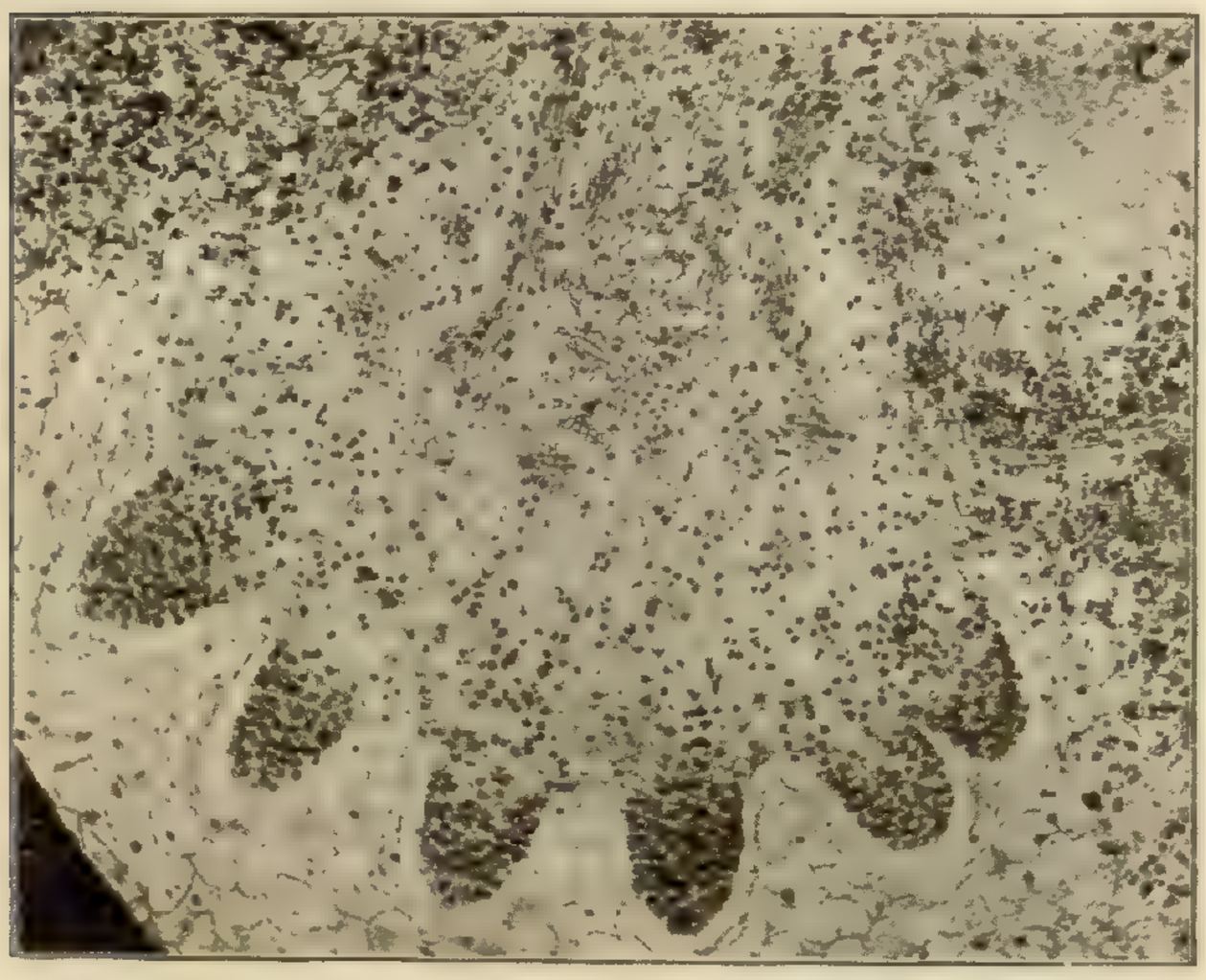

FIG. 2.—Base of bulb, showing inception of roots in summer; ×25.

The number of roots increases with the age of the bulb, in large flowering individuals reaching 30 or 40. These all die at the close of the season, and a new set is formed for the next year, even if the new bulb is developed *in situ*. The roots have no contractile cells, and act only as absorbing organs; the shape of the bulb helps to anchor the plant in place. Root hairs are produced in abundance in a moist chamber, or in nature on those parts of a root which may pass through an air space in the soil. Where the soil is in close contact with the root, the root hairs are inconspicuous or undeveloped (in this connection see **8**, p. 146). The meristem tissue from which the roots arise continues to form new root rudiments for some time after the main supply of roots is formed. Thus a new crop of roots may be formed after the already developed

one has been cut off; or if in handling the bulbs the roots present become dry, new roots are protruded among the bases of the old. In sections young rudiments are to be found in the basal tissue until nearly the close of the growing season.

The roots have a well-developed endodermis, formed of two, or rarely three, cell layers just outside the usually triarch stele (figs. 21, 22). The endodermis is delicate in the seedling, but well developed in the older roots.

The stem apex becomes more active after the roots are established in the soil, and develops the bulb rudiment from the apical bud. There are two axillary buds; one of these is in the axil of the first leaf (cotyledon), the base of which elongated to form the dropper, and on the death of the seedling dried out to form the husk. The other bud is axillary to the inner scale, which forms the bulk of the bulb as it lies in the soil until the second growing season begins. In the primary bulbs neither of these buds ordinarily develops further; but in older plants these, as well as the apical bud, form runners. During the mild periods of the winter and early spring the leaf is protruded from the bulb, and appears above the soil about the middle of March. The first leaves are about 1 cm. in width by 3–5 cm. in length, a little more tapering than the older leaves, but in other respects like them. They last for six to eight weeks, and then disappear by retrogressive withering. During their activity the bulb rudiment at the base of the petiole enlarges to its full size as the secondary bulb.

The starch stored in the primary bulb is used in part in the formation of the aerial structure (foliage leaf), in part also in the building of the new bulb. The bulb gradually disappears as the new bulb develops, the older tissues becoming free from starch and reacting to the Fehling test for sugar as the season advances and the new bulb enlarges. When the leaf begins to wither, in late May, there is practically nothing left of the primary bulb except its husk; this still incloses the base of the petiole, which forms the husk of the secondary bulb. After the death of the foliage leaf, the bulb is dormant until the roots are developed in September, as the first step in the third vegetative season. But in the interval the stem apex organizes the foliage leaf, and organizes the buds

in the axils of the two bulb scales as runner rudiments, in preparation for the next year. The details are similar to the same steps in the primary bulb.

Immature stages

Between the development of the secondary bulb and that of the bulb which bears a flowering shoot, an indefinite number of years may elapse. The least number of intervening seasons has been calculated to be three, making, with the first and second seasons, a minimum of five years from seed to seed. Many individuals at any stage fail to produce runners in any one season, and their immature period is correspondingly lengthened. Others fail to gain any depth in the development of the new bulbs from runners, and these also lengthen the interval between the first and final bulbs. With the production of the flower the activity of the primary stem apex ceases, the subsequent bulbs being developed annually each from a bud at the base of the aerial shoot. In the immature individuals more than one bulb is formed in average seasons in four species,[2] more or less specialized structures being developed for this purpose. Most of the plants producing runners in *E. americanum* in any one season after the second bulb have three at a time. One of these is the apical bud, the other two are axillary buds. The relation of these three buds is shown in figs. 28–33; these buds have been mentioned in a preceding paragraph as related to the development of the runners. The runners in the four species mentioned are not uniform in character, since in the development of the elongated structure of the runner different tissues are made use of by the plant in different species. *Erythronium americanum* is the most specialized in its development, but it is the clearest morphologically.

Each of the runners in *E. americanum* comes from a bud within the bulb (text fig. 3), the buds being made up finally of two scale leaves and a stem apex inclosed by them. The buds are inserted upon the tissues of the bulb in such a manner that the outer surface

[2] These are *E. americanum*, *E. albidum*, *E. propullans*, and *E. Hartwegii;* others rarely multiply. In *E. propullans* the adult plants have a lateral runner in addition to the renewal bulb within the old. Under cultivation axillary buds in adult bulbs in most species develop into bulbs.

of the external scale is united to the subtending portion of the bulb. As the buds begin their development, the first growth is eccentric and pushes the base of the bud outward from its first position, leaving the bottom of the bud free from contact with other tissues. Subsequent growth on the part of the bud is chiefly located in a zone about the base of the scale, close to the insertion of the inner scale upon the base of the bud. As the point at which the bud is united to the bulb tissue is above the zone of growth, the growing zone tends to push the base of the bud away from its original position and downward into the soil, as was the case in the beginning of the dropper. This elongation is confined almost entirely to the outer scale, the inner scale and the inclosed stem

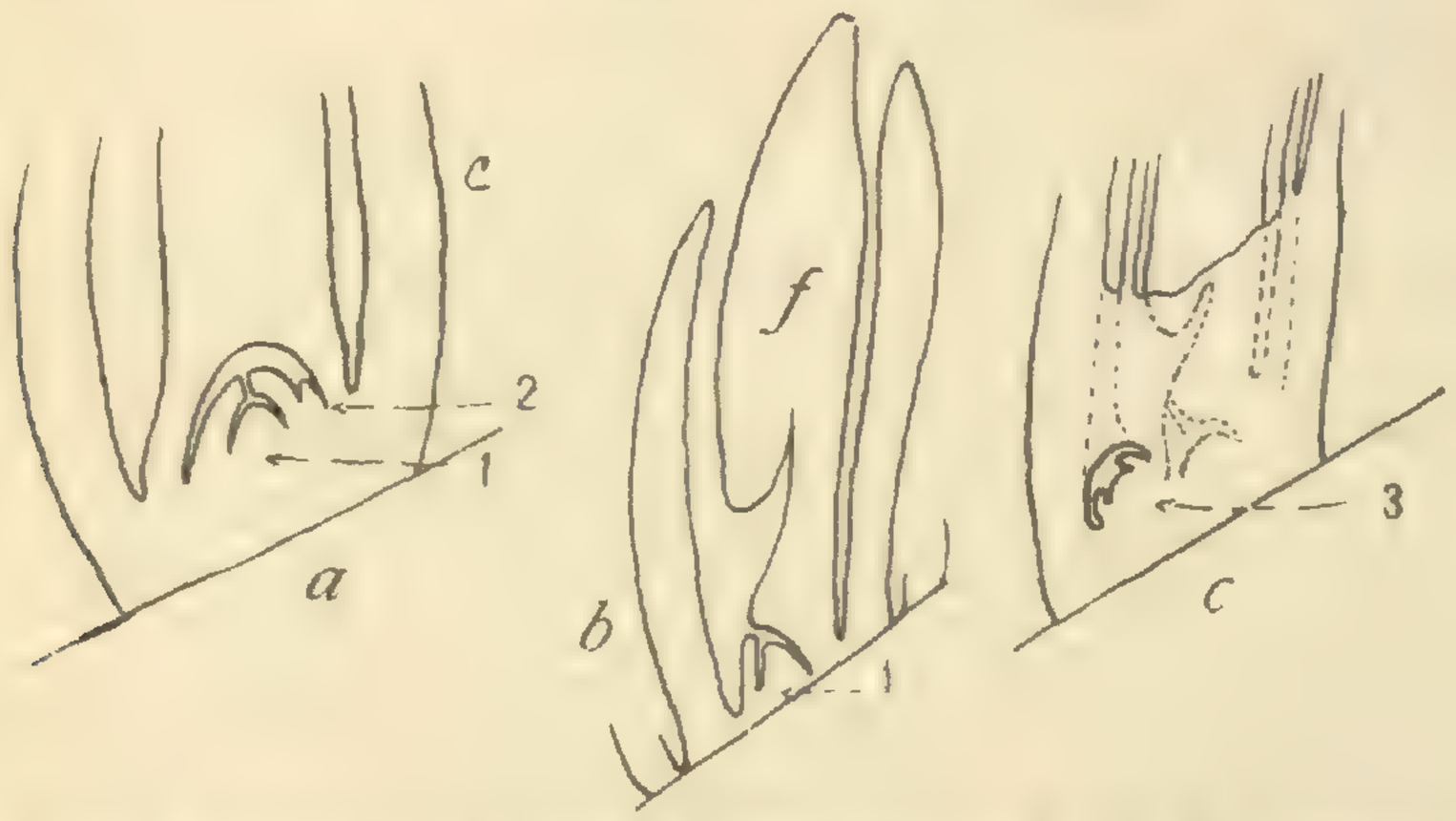

FIG. 3.—Space relations of buds in immature bulb of *E. americanum:* *1*, stem apex; *2*, inner axillary bud; *3*, outer axillary bud; ×10.

apex being carried along passively, as the terminal bud in the runner (cf. fig. 13). The runner is thus formed by the elongation of the outer scale of the bulb rudiment, and in the case of the apical bud and the inner axillary one, they burst through the inclosing base of the petiole when the base of the bulb has been penetrated. In these runners the scale is definitely organized in the bud, before any elongation begins, and the base of the foliage leaf takes no share in the formation of the runner, as did the base of the cotyledon in the seedling dropper. In other species[3] the sheathing base of the foliage leaf contributes to the developing runner, as in the case of the cotyledon and dropper. The elongation in this type of runner is the same as that in *Tulipa* (ROBERT-

[3] *E. albidum* for example.

SON 17, IRMISCH 10), in that the protrusion of the petiole base carries with it the bud inclosed by the petiole sheath.

In *E. albidum* two runners are usual, while the species from the western United States and Eurasia normally form but one. The length of the runner may be so much reduced as to pass unnoticed, but unusual conditions may demonstrate the presence of the typical structures not otherwise distinct. When but one runner is formed, or when the bulb is renewed *in situ*, the main stem apex is the active structure, the axillary buds if present remaining undeveloped.

There seems to be a moisture relation on the part of the growing runners. Plants of *E. americanum* growing in well-drained wood soil were found in several cases to have few runners; while other plants of similar general appearance, but in wet soil at the bottom of the same hill, showed runners in most individuals. It is noticeable about Baltimore that those individuals which grow in heavy, wet soils produce runners earlier and more abundantly than those of drier habitats. The development of abundant runners would hasten the attainment of full depth on the part of a particular group of plants, and this would be manifest in the greater frequency of flowering plants in a colony of stated size. The conditions under which the plants grow are evidently directly related to flower production, as the abundance of bloom has been observed to be associated with abundance of moisture in each of the habitats examined during the work here discussed.

In moist chamber experiments it was found that the tips of the runners were positively geotropic when lying on the top of saturated sphagnum, a little free water being present in the dish (fig. 23). In the absence of free water in the dish, the response was less marked, and in mere dampness it was a negligible quantity. In testing to determine whether the downward growth of the tips under abundant moisture is due to a moisture response or to gravitation, experiments were made with moist sphagnum in different positions in reference to the growing runners. The slow growth and the sluggish response on the part of the runners made the experiments inconclusive. In the moist chamber a period of two or three weeks was needed to carry through a set of tests.

The slow growth of the runners made experiments with them unsatisfactory when using the centrifuge or klinostat, but the evidence obtained tends to confirm the indifference to gravitation noted under natural conditions.

The lateral displacement of axillary buds, with little subsequent elongation, occurs in species of *Gagea* (IRMISCH 10). In *G. minima*, *G. lutea*, and *G. pratensis* there are short protrusions of the bulb rudiment as if about to form a runner, but the elongation is not sufficient to burst through the base of the bulb. The sheath in which the new bulb is formed is the base of one of the leaves, which forms a pouch or pocket about the enlarging bulb rudiment. In *Tulipa* the base of the petiole not only forms the pocket immediately about the bulb rudiment, but elongates in such a manner as to carry the inclosed bud forward into the soil as the terminal bud in a hollow runner. This is the type mentioned above as occurring in *Erythronium albidum* and others in respect to the apical bud. In each of these cases the bud tends to become deeper than its predecessor, but in *Allium vineale* and *A. Scorodophrasum* (IRMISCH 10) the buds are borne upon independent bases, which elongate during the growth of the buds, so that the the buds are elevated from the first position and thrust out of the top of the bulb. In the cases first mentioned the buds are attached laterally to the bulb tissue from which they arise, and are thus unable to rise above their insertion, but must descend more or less sharply in the individual species.

Structure of runners

The structure of the runner may be understood from the accompanying diagram (text fig. 4). Such a bud as that of *Allium vineale*, which elongates in the region below the insertion of the bud scales, would be elevated above its original position; this is the normal erect bud. On horizontal rhizomes a bud assumes the position shown in 2 of the diagram at the close of the period of elongation. If this position were taken during active progress through the soil, a great amount of resistance would have to be overcome in pushing the erect bud forward. This exact arrangement of parts has not been noticed in nature; but it occurs slightly modified in *Erythronium propullans*. In this species the

lateral runner issues from the side of the shoot with the bud at the tip in an erect position. But the bud does not stand freely exposed above the general surface of the runner stalk. The region immediately behind the bud, where the scale and cauline tissue are fused, thickens vertically, so that the bud receives the support of the adjacent tissue for its whole height, and is therefore not subject to transverse strain tending to invert it upon its base.

In the absence of supporting tissue for the height of the bud, the elongating runner would tend to advance the base of the bud

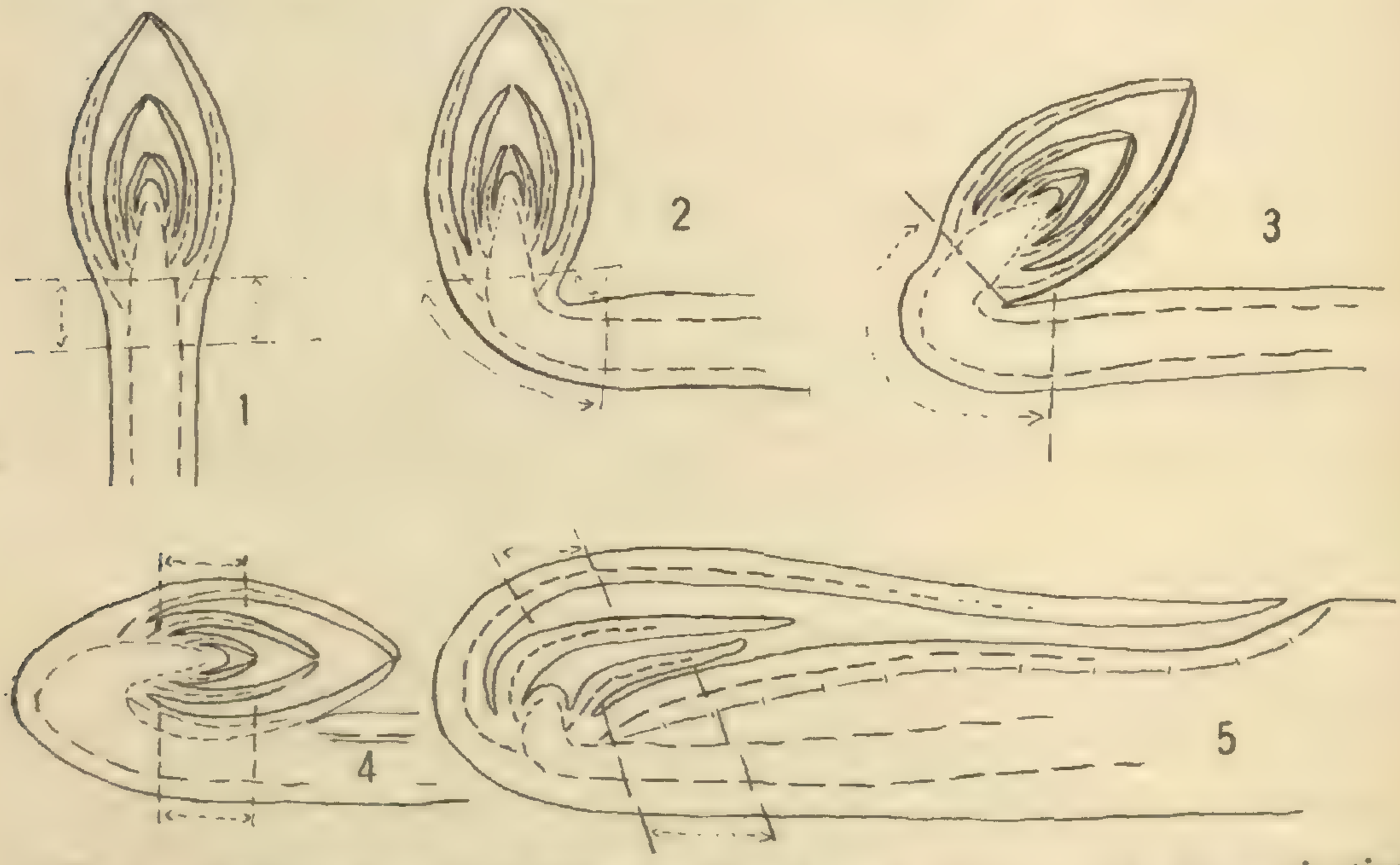

FIG. 4.—Evolution of *Erythronium* type of runner: *1*, normal bud, terminating stem (*Allium*); *2–4*, hypothetical stages, with horizontal stem; *5*, anatropous bud of *Erythronium* runners; dotted lines and arrows indicate zone of elongation in each case.

beyond the rest of the bud, as in no. *3*, since the unsupported parts of the bud would be retarded by friction in passing through the soil. The tendency under such conditions would be for the adjacent surfaces of the bud scale and the stalk to fuse, as suggested in no. *4*. Up to this point the scales of the bud have taken no part in the elongation of the runner or of the bud at the tip; but with the fusion of the bud with the surface of the runner stalk, either the zone of elongation must shift to a point outside the fusion region, or the scales must be included in the growing zone; otherwise the tissues would be under continued but irregular strains. In the

runners of *E. americanum* the structure sketched in no. *5* is present. The zone of elongation is close to the organic base of the bud, while the bud scale is fused for its full height with the stalk of the runner. There are no disruptive strains in this case, for the external scale of the bud elongates as fast as does the cauline tissue of the runner; that is, the scale leaf, like a foliage leaf of the same plant (ROBERTSON 17), elongates in the basal zone; the stem elongates in its apical region, and as the two are folded back upon each other, the two growth regions are continuous about the inclosed bud. The position of this region of elongation is indicated by the space between the diagonal dotted lines in no. 5.

The cauline tissue in the runner is represented by the vascular bundles which unite the terminal bud in the runner tip to the base of the parent bulb. The presence of foliar tissue on the same side of the runner is indicated by the course of the vascular bundles, which turn backward at the base of the scale, and supply the inner face of the axial wall of the dropper in the same manner as the thin abaxial wall, where there is no tissue other than the scale. (Cf. text fig. 1.)

The runner habit

The plumule (stem apex) in the cotyledonary sheath does not form any bud scales which might by their elongation produce the dropper; but the walls of the cotyledonary sheath elongate after the primary root is established, and develop the dropper with the plumule as the terminal bud therein. This appears to be constant for all the species of the genus. In the subsequent stages in the several western species, and in *E. albidum* and *E. mesochoreum*, the main stem apex is thrust out as the runner bud within the elongated sheath formed by the clasping petiole. This is exactly comparable to the dropper of the seedling, in that the bud is carried forward passively and contributes nothing to the development of the structure. In the case of the second runner of *E. albidum* and of each of the three runners in *E. americanum*, the runner is formed by the bud itself forming the runner sheath by the elongation of its outer scale. The development of this type of runner introduces a new structure into the series present in the life cycle of the other species, and the degree to which this

innovation is developed may be taken as an index to the divergence from the original type. On this basis the most divergent species is *E. americanum*, with *E. albidum* and *E. mesochoreum* in order toward the type. *Erythronium propullans* is a special case, in which the bud axillary to the foliage leaf (text fig. 3, bud *2*) in immature plants (as of *E. americanum*) is functional in the mature individuals, being elevated above the base of the bulb by the growth at the base of the aerial shoot, as this raises the base of the leaves to their final position. In floral characters it is most nearly related to *E. albidum*. The reduced size of the flower is probably

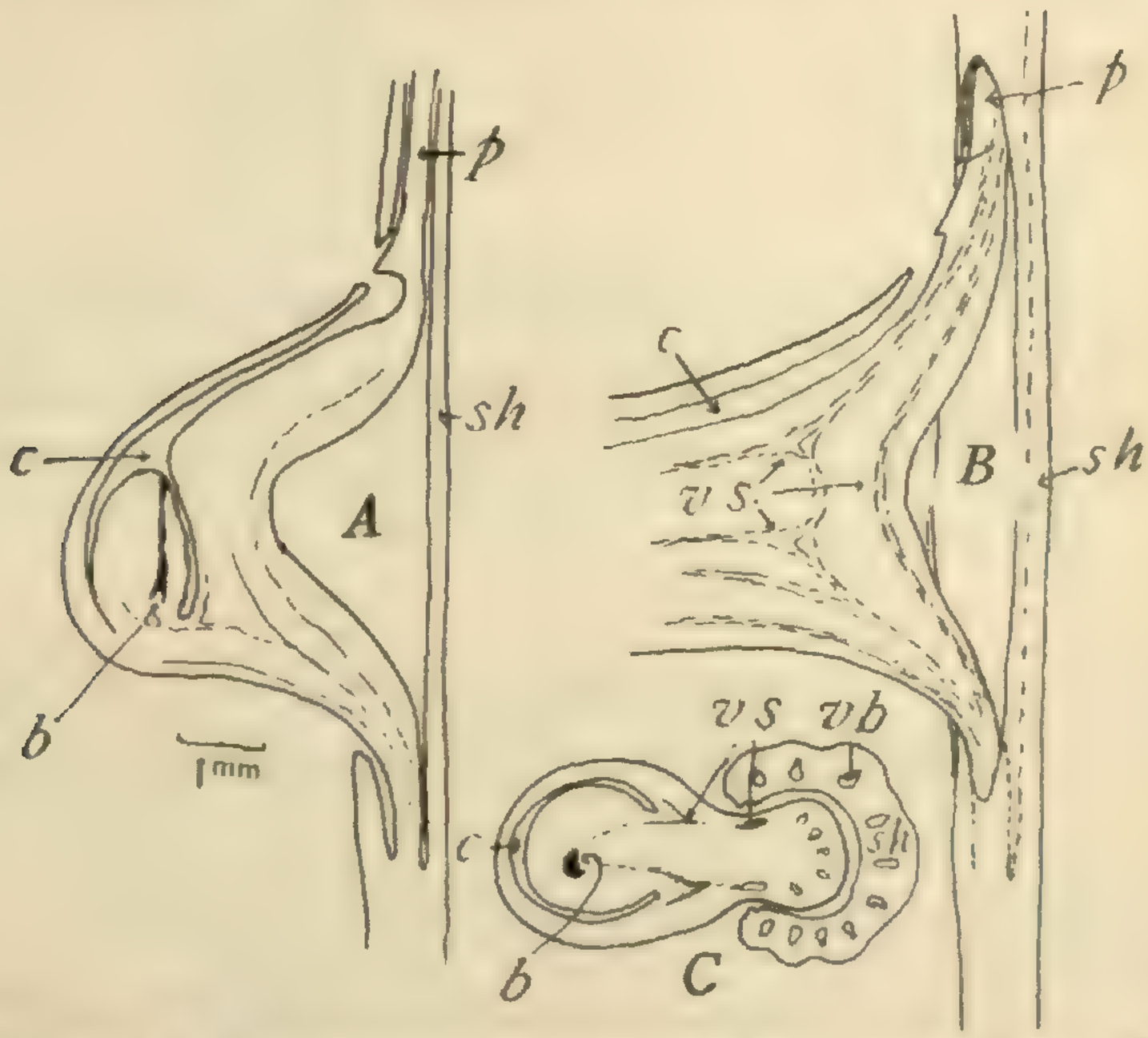

FIG. 5.—Offshoot of *E. propullans*, showing structure and vascular elements in sections: *A*, *C*, on base of older offshoot *B*; *b*, bud of offshoot; *c*, cavity about bud.

due in a measure to the interference with normal nutrition of the flower caused by the diversion of a portion of the vascular supply of the peduncle into the developing runner. The bud from which the lateral runner develops is inserted on the base of the peduncle in such a manner that in the early stages of growth as a runner the base of the peduncle elongates and thickens. As the clasping petioles (*sh*, text fig. 5) hold the upper part of the peduncle from freely moving upward, the result of elongation is to form an elbow, with the bud at the convex side of the bend. At this stage all the vascular bundles are diverted with the general distortion of the base of the peduncle (*A*). As the runner pushes forward from the

elbow of the peduncle, certain of the peduncle bundles produce branches which grow with the advance of the bud and maintain connection with the main vascular supply of the plant (*B*); but in so doing the total supply available to the peduncle is divided between the runner and the peduncle itself, and the reduced size of the flower appears to be the result.

In the species east of Colorado the aerial portions of the plant disintegrate with the ripening of the seeds, the fruit being prostrate when the seeds are ripe. The species of the Rocky Mountain region and westward do not become prostrate, but as the fruits ripen the stalk becomes a stiff and elastic wand, from the top of which the seeds are shaken. In these the capsule is revolute only at the apex, in the others the capsule splits completely to the base; among the first species the seeds are thrown out of the capsule by shaking; in the second group they are released by the rolling back of the inclosing walls of the prostrate capsule. The Eurasian species *E. Dens-canis* belongs to the second group in respect to its seed dispersal.

The western species differ from the forms of the eastern states in details of bulb development. In the eastern forms the region of fusion between the bulb tissues and those of the bud is small; and the sheath inclosing the bud, either in the case of the runner bulbs or when renewed *in situ*, is free from the developing bulb for most of its surface; but in the western forms the elongated bulb has a long fusion zone along the axial side, where the base of the sheath and the surface of the inclosed bud scale are fused. This appears as a ridge, from the edges of which the husk, in fully formed bulbs, extends around the rest of the bud. The bulbs are as a rule much more attenuate in the western forms than in the eastern, both in the young and in the adult stages. In immature bulbs the tip of the new bulb is often not at all lower than the base of the preceding bulb; this is due to the elongation upward on the part of the bud scales at a rate equal to that of the descent of the base of the new bulb in the petiole sheath. In the older bulbs the descent is decreased, but the elongation of the bulb scales upward from their bases produces the long bulbs characteristic of the group. In the bulbs examined, the species

from the western states have thinner husks than those of the eastern states, except *E. Hartwegii*, which has a tough and thick one like that of *Tulipa*. This form grows in an adobe soil, subject to high temperatures and considerable pressure when the soil dries, which may have its influence in the development of the heavier husk (WARMING **22**). The Eurasian species (*E. Dens-canis*) has a very delicate husk, which becomes fragmentary during the development of the new bulb, so that the bulb is but slightly protected. The development of the bulb in this species is similar to that of the western forms, but the zone of fusion on the axial side of the bulb rudiment is more nearly the full height of the bulb scale than in these, extending almost to the tip of the scales, and the stem scar seems to be at the apex of the scale. As a result, the scales are fused together along their adaxial surfaces and the axillary buds are inserted much farther from the base of the bulb than is the case in any other species. The base of the petiole becomes charged with starch, and indistinguishable in appearance or function from a bulb scale. This explains the absence of a husk, formed in the other species from the drying of the sheathing petiolar sheath. The seedling of this species is similar to that of the rest of the genus, but there seems to be less of deepening growth in the immature stages than in any of the species of the United States. It is probable that the period of blooming is attained even more slowly by *E. Dens-canis* than in the other species, if the same relation of depth and flower production is maintained. In some of the western species grown in the Botanical Garden of Johns Hopkins University, it was noticed that they bloomed when the bulbs were much smaller in proportion to the average mature size than do those of the eastern forms. It may be that the same early blooming is present both in the Eurasian and in the western species, and that the bulbs continue to descend gradually during a long period after the blossoming habit is inaugurated. Such a point is physiological rather than morphological, and will not be discussed further at this time.

In the runners of *E. americanum* occasional "stimulation growths" have been noticed, apparently related to sudden excess of water. These are due to the bud inclosed by the runner bursting

through the tip of the runner, just as the runners burst the petiole sheath when first issuing from the bulb. The next scale of the bulb rudiment forms the runner extension, and the stem apex with a small scale is carried forward as if under normal conditions. The necessary nourishment for the added growth comes from the parent plant, through the stalk of the runner to the point where the terminal bud was inserted. Then the vascular bundles of the bud, following down through the bud scale, convey material to the stem apex in the tip of the extension of the runner. In two cases, in the spring of 1908, this extension of the runner by the protrusion of the terminal bud through the end of the runner sheath had been repeated a second time.

Development of the mature plants

The production of the flowers, which mark the maturity of the individual plant and the termination of the cycle of stages from seed to seed (text fig. 6), is associated with several changes from the manner of development followed during the immature condition. During the whole period from seedling to this stage, the primary stem apex has persisted, and from it have come the successive leaf rudiments which developed into either bulb scales or foliage leaves as the conditions demanded. The accompanying tabular view of the activity of the primary stem apex will show the general relation of these leaf rudiments. In addition to the outgrowths from the apical dome in the form of leaf rudiments, there have been various buds, axillary to the inner scale, which were laid down by the stem apex from time to time. The leaf rudiments developed in these axillary buds are not considered in the tabulated series of products from the stem apex. The bud in the axil of the outer scale does not arise from the apical tissue directly, but from the mass of meristem at the base of the scales.

The final structure developed from the primary stem apex, after passing through the immature stages, is the flower bud of the mature individual. In the immature stages the apical dome persists at the base of the bulb, producing successively the several bulb scales and foliage leaves. In the mature bulb the apical dome becomes surrounded by the foliage leaf rudiments (fig. 25),

and the whole structure becomes elevated above its original position by the elongation of the tissue below the insertion of the leaves. In the production of the flower bud, at the summit of the aerial shoot, the original stem apex comes to an end. The renewal bud for the next bulb is formed as a bud in the axil of the inner bulb scale, at the base of the shoot (figs. 25*b*, 26, 27).

GENERAL SEQUENCE OF FOLIAR OUTGROWTHS FROM THE STEM APEX IN ERYTHRONIUM AMERICANUM

Vegetative period	Foliar structures				Bulb sequences
	Sequence	Character	Function	Fate	
First	First leaf	Cotyledon	Photosynthesis	Withers	
	Second leaf	First scale	Dropper	Husk	Primary bulb
	Third leaf	Second scale	Storage	Bulb scale	
Second	Fourth leaf	First green leaf	Photosynthesis	Withers (husk?)	
	Fifth leaf	Third scale	Storage	Outer scale	Second bulb
	Sixth leaf	Fourth scale	Storage	Inner scale	
Third	Seventh leaf	Second green leaf	Photosynthesis	Withers*	
	Eighth leaf	Fifth scale	Runner	Husk	Third bulb
	Ninth leaf	Sixth scale	Storage	Bulb scale	
Fourth	Tenth leaf	Third green leaf	Photosynthesis	Withers*	
	Eleventh leaf	Seventh scale	Runner	Husk	Fourth bulb
	Twelfth leaf	Eighth scale	Storage	Bulb scale	
Fifth	Thirteenth leaf	Fourth green leaf	Photosynthesis	Withers*	
	Fourteenth leaf	Ninth scale	Storage	Outer scale	Fifth bulb
	Fifteenth leaf	Tenth scale	Storage	Inner scale	
	Sixteenth leaf	Fifth green leaf	Photosynthesis (and flower stalk)†	Withers	

* If the bulb is renewed *in situ*, the base of the leaf becomes the husk of the new bulb; if the new bulb develops as a runner bulb, the runner sheath forms the husk.

† With the development of the floral axis the activity of the primary stem apex ceases, a branch apex forming the renewal bulb thereafter..

This bud is evidently the homologue of bud *2*, of the immature stages, as indicated in text fig. 3. The bud is at first distinctly in the axil of the scale, but with the upward growth of the adjacent shoot it is lifted from its position to one on the base of the shoot itself (figs. 27 and 29, *3*).

The apical dome of this bud develops bulb scales during the

summer and develops into the full-sized bulb during the active period of the aerial shoot at the base of which it lies. Starch for storage is derived both from the photosynthesis of the leaves and from the deposits in the old bulb within which the new bulb

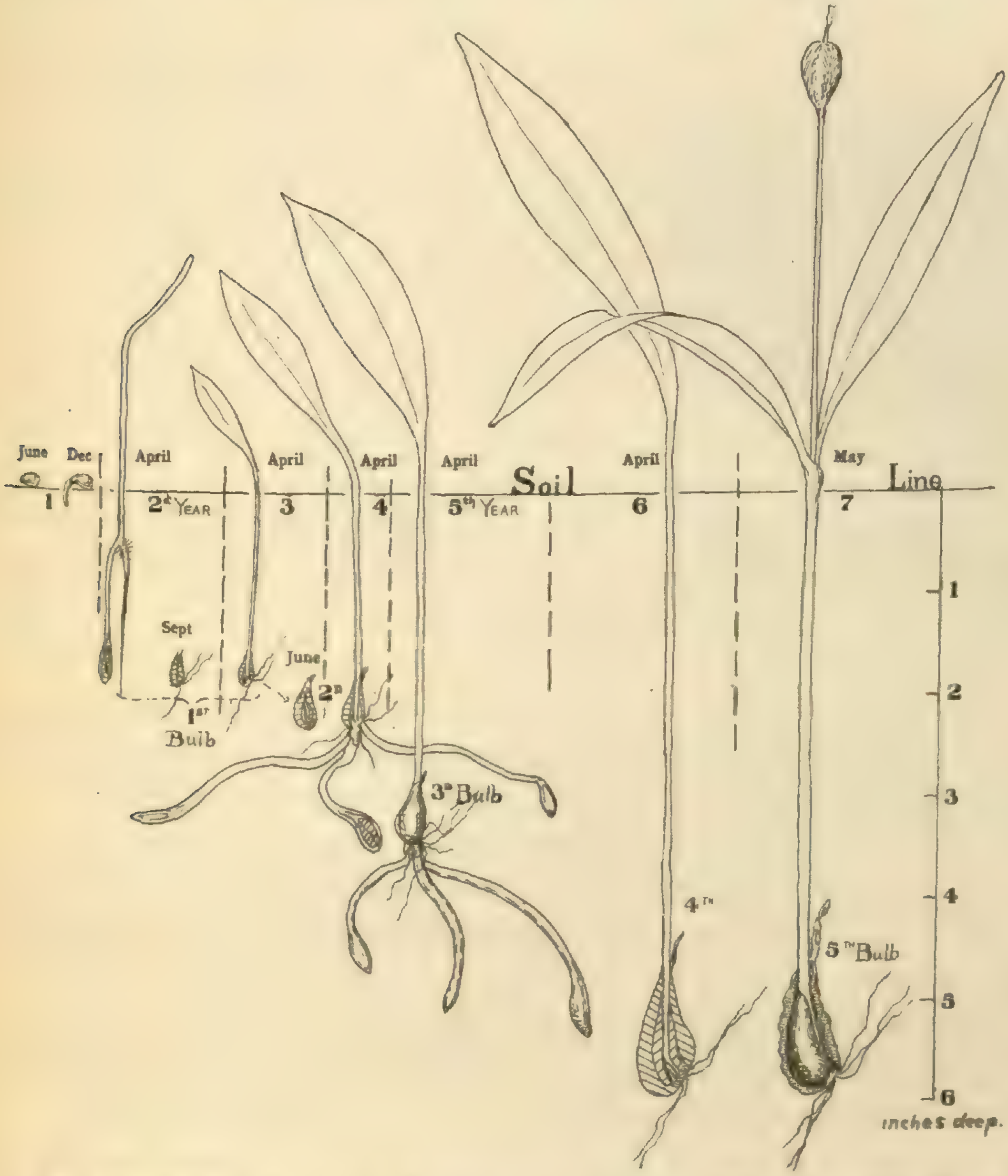

FIG. 6.—Stages in life cycle of *E. americanum:* under natural conditions the third bulb may repeat itself indefinitely, gaining little in depth, being renewed *in situ* for one or more seasons.

is formed. By the time the aerial shoot is dead, the new bulb is mature, and the apical dome within it lays down the rudiments of the next flower. This process is repeated indefinitely, the

individual becoming more robust with time, but otherwise remaining the same. A very slight increase in depth occurs as time passes, since the new bulbs are a little larger than their predecessors, and the new bulb is formed below the center of the old one which it replaces. But a bulb once flowering may revert to the sterile condition after a series of years. Bulbs which have been dug from the soil and allowed to become somewhat dried out are apt to "break," that is, to produce two or three small bulbs instead of the single large one customary in the flowering plants. Bulbs so produced are sterile for at least two years, as found by experiment. This is especially apt to occur if the bulbs are dug while the shoot is actively growing upward through the soil in the spring. Removal of the soil close to a bulb of a flowering plant often causes such to revert to the immature condition and produce runners, even though the flowering of the current season is not hindered by the changed soil conditions.

Individual plants of any age may force the bulb rudiments into abnormal development under the stimulation of unfavorable conditions. A large number of bulbs of various sizes were dug soon after the leaves had pushed through the soil. These with a little soil were left in a tin box for several days; the box was well wrapped and left in a cool room in the meanwhile. Upon inspection ten days later, the leaves were found to have shriveled away, but the bulbs had formed a small bulb from each of the buds which under normal conditions would have developed runners. The starch present in the old bulb and in the leaf furnished the material for the new bulbs, aside from water, which was in the moist soil. This was repeated several times, the exact details varying with the exact condition of the bulbs when dug from the soil. Thus if the runner is already pushing through the base of the bulb, or is further developed, it continues to elongate for several days, but in the end will form the terminal bud into the bulb; it apparently transfers to it the substance of the old bulb and runner stalk as if under normal conditions.

In the descriptions of the liliaceous ovary, the placentae are usually said to come from the incurved margins of the carpellary leaves. In *Erythronium*, however, the margins of the carpels

appear to come into blunt contact, but do not curve inward. The margins unite along the line of contact, and the partitions are formed from a median rib projecting inward from each carpel (figs. 34, 35), meeting at the center of the ovary (TEMPLE 21). In the full-grown ovary, as at fertilization, the evidence for this interpretation of the case is found in the double bundles along the line of dehiscence in the walls of the ovary, and in the presence of a layer of cells rich in protoplasm which passes around the end of the abutting partitions as they come into contact at the center of the ovary (text fig. 7). The densely protoplasmic cells which line the ovary along the line of the placentae continue around the end of each median wing, as shown in the photograph. This series of surfaces of slight contact determines the dehiscence of the ripe capsule.

FIG. 7.—Transverse section of fertilized ovary of *E. americanum*, showing abutting placentae (*p*), two-celled embryo (*e*), and double bundle at edges of fused carpels (*b*); ×25.

Occasional plants are found with sterile anthers on one or more of the stamens, some patches showing many of the plants with no functional pollen. It has been found that the sterility of the anthers begins at least as early as the divisions of the pollen mother cells, as buds have been examined in which three of the anthers were normal, and had normal pollen grains; while the sporogenous tissue of the others was degenerating (fig. 35, *m*, *m'*); the other tissues of the anthers were normal in appearance. In the field it has been noticed that the plants with dark pollen on the stigma had the larger fruits and the larger number of seeds. Plants having pale anthers often lacked pollen entirely, and their seed-developing power seemed to be deficient also. The plants of the two types, fertile with dark stamens and poor with pale anthers, each occur in patches often of considerable numbers. This may

account for the poor set of seed in such cases, for insects working over the patch would not bring in so much viable pollen to the weak plants as if there was a commingling of the two.

Development of seeds

The fertilized ovule enlarges rapidly, mainly through the growth of the embryo sac. The sac destroys the nucellus except a crushed remnant at the bottom of the sac. The raphe and chalazal spur enlarge at the same time, and add to the bulk of the seed as a whole. The endosperm develops slowly, remaining for a considerable time as a layer lining the wall of the sac between the base and the suspensor at the tip. The embryo first develops a considerable mass of cells in the micropylar end of the sac, from the inner free surface of which the functional embryogenic cells are developed (COULTER 7). This inner surface may become lobed, and then gives the condition called polyembryony by JEFFREY (13) and SCHAFFNER (20). Twin embryos developed in one case out of several hundred seeds germinated in this work; these were united near the upper end, but completely free below, and their vascular systems were distinct. These embryos probably were formed from two adjacent lobes from the free surface of the suspensor, becoming united through the incorporation of some cells in common from the base of the lobes. In pushing into the soil, the elongation had occurred in the zone just behind the stem apex, and this was distinct in each of the two embryos, producing the condition shown (fig. 36).

The general conditions of the sac, endosperm, and suspensor in *E. americanum* are closely duplicated in *Urtica cannabina*, as studied by MODILEWSKY (15). In both cases there is a thin lining of free endosperm nuclei along the walls of the sac, a considerable suspensor at the tip, and a mass of deeply staining cells below the base of the sac. In *Erythronium* these cells form a considerable mass, and extend backward to the termination of the raphal bundle at the chalaza. These cells stain deeply even in ripe seeds, and the adjacent cells of the remnant of the nucellus remain in close contact with the center of the base of the endosperm in the ripe seed. This would indicate the purpose of these cells

to be that of transfer agents for substances from the chalaza to the embryo sac, and thence to the forming embryo and endosperm.

When the seed reaches its full development the embryo sac is filled with hard endosperm of reserve cellulose. The cells in the endosperm have their longer axes directed inward from the periphery, curving somewhat toward the micropylar end of the seed. Through the center of the endosperm there is sometimes the same cellular endosperm as elsewhere, more frequently this is nearly solid cellulose. Immediately about the embryo there is usually a small mass of less firm endosperm, which in some cases extends to the surface of the seed, filling the space earlier occupied by the suspensor. It is probable that germination is aided materially in such cases, as moisture can more promptly reach the embryo by this path than would be the case if only thick-walled endosperm were present. At the base of the seed the endosperm shows considerable shrinking, with the remnant of the nucellus remaining in contact with the endosperm for a small area near the center. This secures contact between the hard endosperm and the spongy spur, and even when the spur has disappeared the inner layers of the tissue at the chalaza remain in intimate contact with the base of the endosperm. As the endosperm along the axis of the embryo sac is the last to be deposited, it is probable that the mass of spongy cells in contact with the base is of advantage in the imbibition of water preliminary to germination. In different seeds the exact appearance of the central portion of the endosperm varies from nearly solid, with infrequent cell cavities, to a condition similar to that of the peripheral endosperm; the latter is less common than is the solid core mass. The exact distribution of the cell cavities in the endosperm is probably in close relation to the moisture conditions during the late stages of ripening of the seed. In germination the embryo first enlarges to occupy the space filled by the spongy endosperm in which it lies; then the cotyledon, acting as a haustorial organ, dissolves a path for itself along the axis of the endosperm. The solvent action extends along the lines of cell cavities toward the periphery, and the endosperm is absorbed almost completely.

Completion of the cycle

The individual which began with the germination of the seed and the organization of the stem apex in the sheath at the base of the cotyledon, has been followed through the series of changes normal to its development as *Erythronium americanum*, and the variations have been indicated between this species and the others of the genus. The cycle of the sporophytic generation is thus completed, and the original stem apex culminates in the formation of the flower parts of the first blossom produced by the bulb on reaching maturity. It was shown that the species were structurally related with a large group, the western species, behaving similarly, the others diverging more or less from the habits of these forms. The structures involved in the divergence from type are those most active in the immature stages, and most freely produced in *E. americanum*. This species, therefore, has been regarded here as the most remote from the ancestral form, since the majority of the species are of the more simple type of development in the vegetative habits. The species having the uniform vegetative habits are native to the region from the Rocky Mountains westward, becoming more abundant in species as the Pacific coast is approached, and culminating in a series of habitats in southwestern Oregon. This may be assumed to be near the original home of the genus, from which the distribution and differentiation into the present habitats and species have occurred. It is probable that the lines of migration have followed the present lines of specific distribution, especially in the United States. The single species of Eurasia combines the bulb characters of the western species with the withering aerial parts of the eastern forms. The character of the habitats in which this species occurs may be so nearly uniform that no marked variations have been developed from the original type, beyond that involved in the prostrate fruit. Ants have been observed carrying the seeds of *E. americanum*, and it is probable that they aid in distribution in each of the species having seeds with fleshy raphe or spur tissue. This would include *E. Denscanis* as one of the myrmechochorous species, as a considerable chalazal spur is present, comparable to that of *Viola* or *Sanguinaria* (BEAL 1), but not so large as that of *E. americanum* or *E. albidum*.

Summary

The points presented in this paper may be summarized as follows:

The undifferentiated embryo begins to elongate in the fall and organizes a rudimentary stem apex in a narrow cavity at the base of the cotyledon. In germination the radicle is thrust into the soil during the winter, the stem apex following immediately behind the base of the radicle, in the cavity mentioned. The hypocotyl is represented by the fusion region between the vascular supply to the stem apex and the main vascular system of the seedling; it takes no part in the development of the seedling. After absorbing the endosperm, the cotyledon is elevated into the air, and acts as the first photosynthetic organ. Either two or three vascular bundles are present, varying with the species.

During the activity of the cotyledon as a leaf, the cavity in the base of the cotyledon about the stem apex elongates to form a slender sheath, with the stem apex inclosed as a terminal bud at the tip. The "dropper" so formed is positively geotropic in response, as is the primary root; the runners and roots of later stages are not positively geotropic. At the close of the season the terminal bud of the dropper is isolated in the soil by the withering of other parts of the plant.

During the summer the first foliage leaf is organized by the stem apex and becomes functional the following spring. Roots are protruded at the base of the bulb in the fall, which marks the beginning of the second vegetative period. This sequence of development is repeated in the subsequent seasons to the mature bulbs.

The stem apex becomes inclosed by the base of the foliage leaf, and there forms a bud from which the next bulb will develop. When the bulb is renewed *in situ*, only this bud develops; this is also the rule in the species producing but one runner. In *E. americanum* two buds are usually formed in addition to the main bud, each of which elongates as a runner and forms a bulb. These additional runners spring from buds axillary to the leaf, or to a bulb scale. When but one runner is developed normally by a species, it is formed from the elongation of the base of the petiole, which carries the bulb rudiment into the soil as a terminal bud,

as in *Tulipa*. The additional runners when present, and all three in *E. americanum*, are developed from the elongation of the outer scale of the bud, the inner scale and the apical dome forming the terminal bud of such a runner.

The vascular connection between the stem apex and the point of insertion of the runner is to be considered cauline, the rest of the runner tissue as foliar and apical. The structure of the runner in *E. americanum* is that of an anatropous bud, the outer surface of its external scale being fused with the upper surface of the supporting stem; the latter maintains vascular connection between the base and the apex of the structure developed. The zone of growth of the fusion structure is located as in normal rhizomes, close to the tip of the structure; both the scale and the cauline tissue take part in the elongation.

The mature plants form the floral shoot from the stem apex, the new bulb being developed from a bud, at the base of the shoot. The stem apex of the new bud forms the next flower, and the bulb is renewed in turn from a bud axillary to the inner scale of the bulb rudiment. The bud in the axil of the outer scale usually dies without developing.

Using the runner habit as the basis of comparison, the genus is divided into two groups, one occurring typically at low elevation, and producing two or three slender runners from short bulbs, the other at higher elevation and forming but one runner and developing into slender bulbs. A form intermediate between the two occurs in western Kansas and Nebraska. An aberrant form occurs in a restricted locality in Minnesota, having a lateral runner developed from a bud in the axil of a foliage leaf.

The interval between germination and flowering on the part of an individual is at least six years. This minimum is liable to indefinite increase under average conditions, by the interpolation of additional immature bulbs because of the formation of the runner bulbs no deeper than the parent bulb, or by the suppression of runners in a particular year.

The distribution of the species points to the Pacific coast as the probable home of the genus, the present distribution being the result of migration along lines connecting the habitats of the

present forms. The species are found to vary from the type found in the assumed original habitat approximately in proportion to the distance of migration. The species of Eurasia combines features of the two groups in its vegetative characters.

The roots radiate from a point near the base of the bulb, but show no definite response to gravity; they maintain a definite space relation to each other, defining the surface of a cone in the soil, the axis of which is about 45° to the vertical. In development, the roots arise in September from cells just below the vascular base of the bulb, and grow in straight lines during their elongation. In penetrating the bulb tissue, the cells are apparently dissolved by the root tissue, making a cavity about the advancing root rudiments. The number of roots increases with the age of the bulb.

Conclusions

From the foregoing study the following conclusions may be drawn: The delayed development of the embryo is associated with a large store of endosperm; this is drawn upon by the germinating embryo during the season when vegetative activity is low; the young seedling is established in the soil early in the spring, the endosperm furnishing the needed materials for its development. With the exhaustion of the reserve material of the seed, the primary root is developed, and the cotyledon is elevated into the air and light; the cotyledon is the only leaf exposed to the light by the seedling. The stem apex, located in a narrow cavity in the base of the cotyledon, is carried forward by the elongation of the embryo, and, after the elevation of the cotyledon, is carried farther into the soil by the elongation of the walls of the cavity. The short period of vegetative activity, and the prompt descent of the stem apex in the dropper, would indicate adjustment to short growing seasons; the brevity of the active season is a feature of the life cycle. The tendency on the part of the seedling to bury the stem apex deeply is continued by the immature plants in the production of runners; in some cases these are strictly comparable to the dropper of the seedling in structure, in others they involve new developments; but the result is the same in either case.

The persistence of the original stem apex until the establish-

ment of the flower axis allows for the repetition of an indefinite series of immature bulbs, formed from runners or *in situ*, but introducing no new structures during the whole period of immature development. With the formation of the flowering shoot, the vegetative structures become secondary in importance, and the renewal bulb is developed from an axillary bud at the base of the shoot. The continuation of the individual is thereafter without vegetative multiplication normally, the increase being secured by the seeds.

The geographical distribution of species and their relation to each other in structural details indicate that the genus originated in that region of the Pacific coast now included in the state of Oregon, and has been distributed along lines approximately following the present habitats of the several species. In the progress of migration the advancing species developed special methods for rapid descent into the soil, which in some forms has become a means of numerical increase.

In the development of means of vegetative multiplication, elongation of the structure immediately about the stem apex (in the seedling the base of the cotyledon, in the western forms the base of the petiole) was followed by the elongation of the scales of axillary buds, thus forming additional descending axes, each of which developed an additional bulb from its terminal bud. One species has developed a runner from a bud axillary to the foliage leaf, apparently being derived from the adjacent form in which the second runner arises from a bud axillary to the inner scale. The production of this lateral runner is confined to the flowering plants, since only in these is the leaf axil elevated above the base of the bulb. This form is very restricted, and appears to be the species most recently derived from the parent stock, or from some other species as these are now known.

The general development in the genus would confirm the assumption that it is related to *Tulipa*, especially through *T. sylvestris*.

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EXPLANATION OF PLATES VIII–X

PLATE VIII

All figures drawn on the same scale, which is indicated by the measured line; drawings made by means of a vertical projecting lantern from the stained sections.

Fig. 1.—Dormant embryo in endosperm; *i*, remnant of inner integument.

Fig. 2.—Embryo about December 1, still within seed; *s*, position of stem apex; *e*, endosperm.

Fig. 3.—Descending tip of seedling; stem apex in slit at *a*.

Fig. 3*a*.—Cross-section of seedling at line *a–b* of fig. 3.

Fig. 4.—Tip of cotyledon in longitudinal section, showing haustorial cells (*h*) and vascular cells (*v*).

Fig. 5.—Cross-section of cotyledon; *v*, vascular bundles; *s*, stomata.

Figs. 6–13.—Stages in the development of the dropper about the stem apex (*s*).

Figs. 11, 12.—Two sections of the same dropper, showing scale leaf (*l*) and stem apex (*s*); *t*, plumule trace.

Fig. 13.—Stem apex as terminal bud in tip of active dropper, as in April.

PLATE IX

Magnification the same as in plate VIII, except in figs. 21, 22, 23, 25, in which the magnification is indicated.

Fig. 14.—Stem apex in late June at bottom of bulb.

Fig. 15.—Stem apex (*s*) and rudiment of foliage leaf (*l*) in July.

Figs. 16–20.—Cross-sections of young dropper, from base of cotyledon downward, showing hypocotyl region (17), separation of root and dropper (18), and dome of stem apex (20).

Figs. 21, 22.—Cross-sections of active and dead root steles; *e*, endodermis; ×250.

Fig. 23.—Active runner marked to show zone of maximum elongation after three weeks' growth; natural size.

Fig. 24.—Base of bulb, showing sheathing petiole (*p*), stem apex (*s*), and root rudiment (*r*), as found August 1.

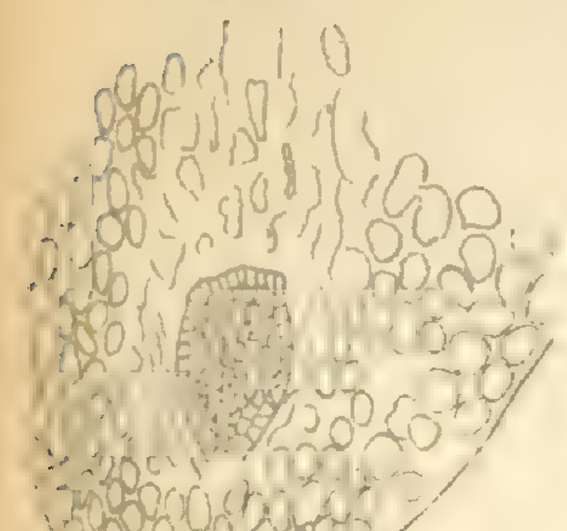
Fig. 25.—Outline of stem apex in flowering bulb, showing flower rudiment (*f*) inclosed by the foliage leaves (*l*) and the location of the renewal bud (*b*); ×10.

Fig. 26.—Renewal bud from the same section showing apical dome above and root rudiment below the scale; July 1.

Fig. 27.—The same structures about August 1, on the same scale.

PLATE X

Figs. 28, 28*a*, 34, 35 on a uniform scale, the same as in previous figures; figs. 29–33, 36 as indicated.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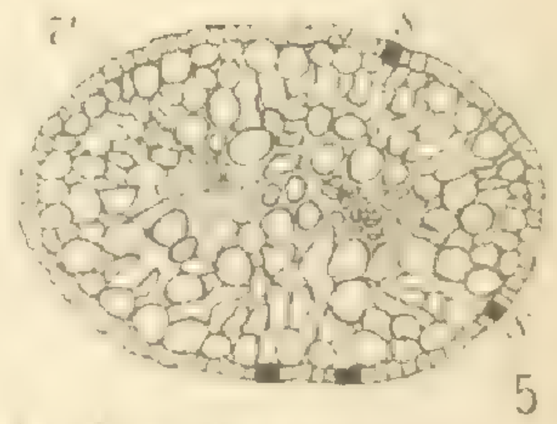
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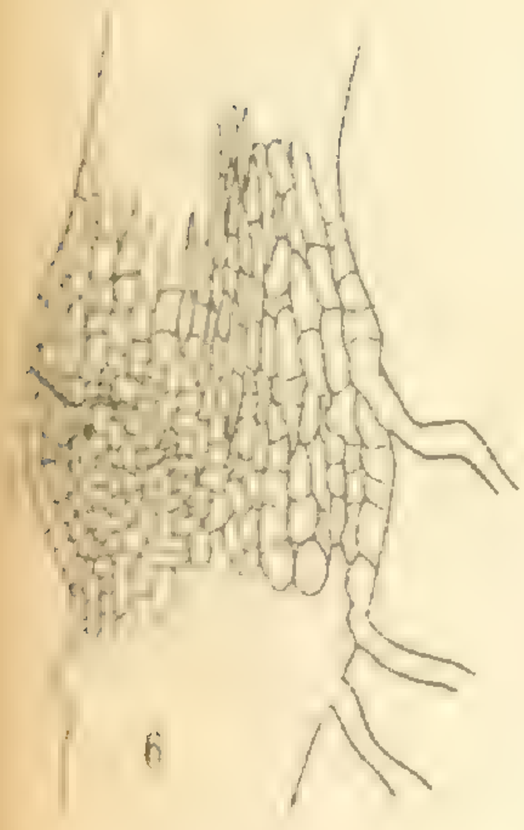
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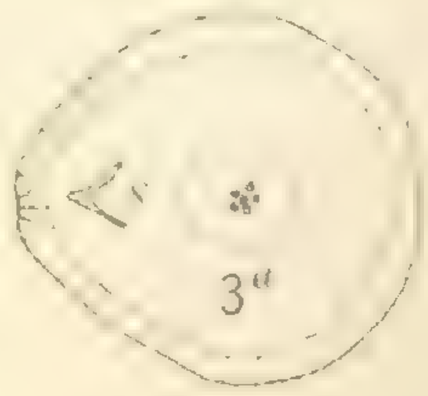

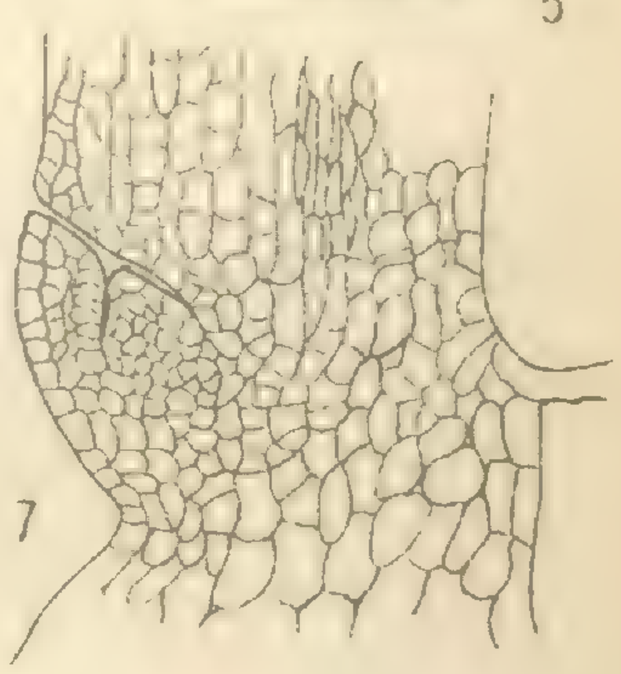
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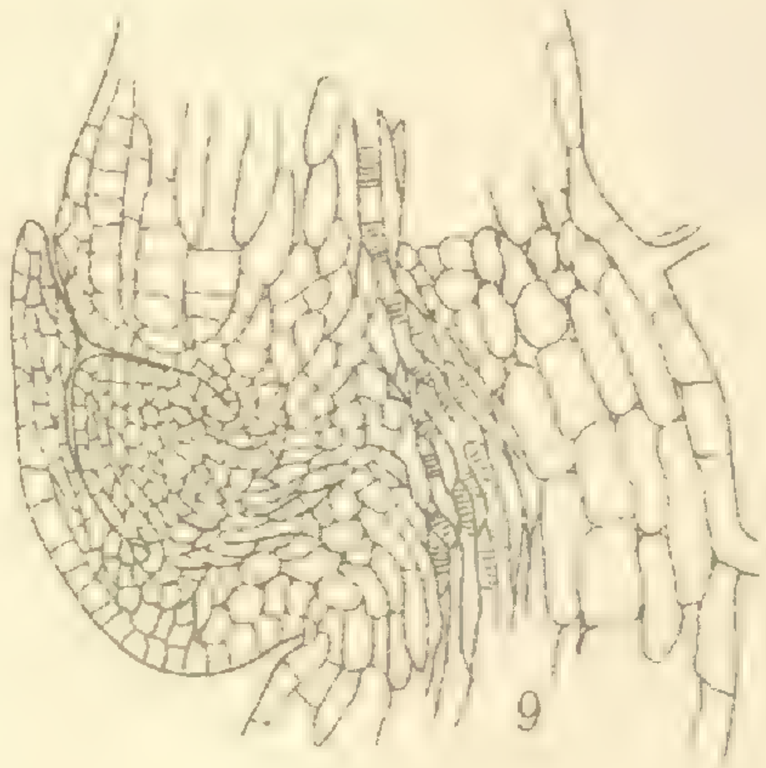
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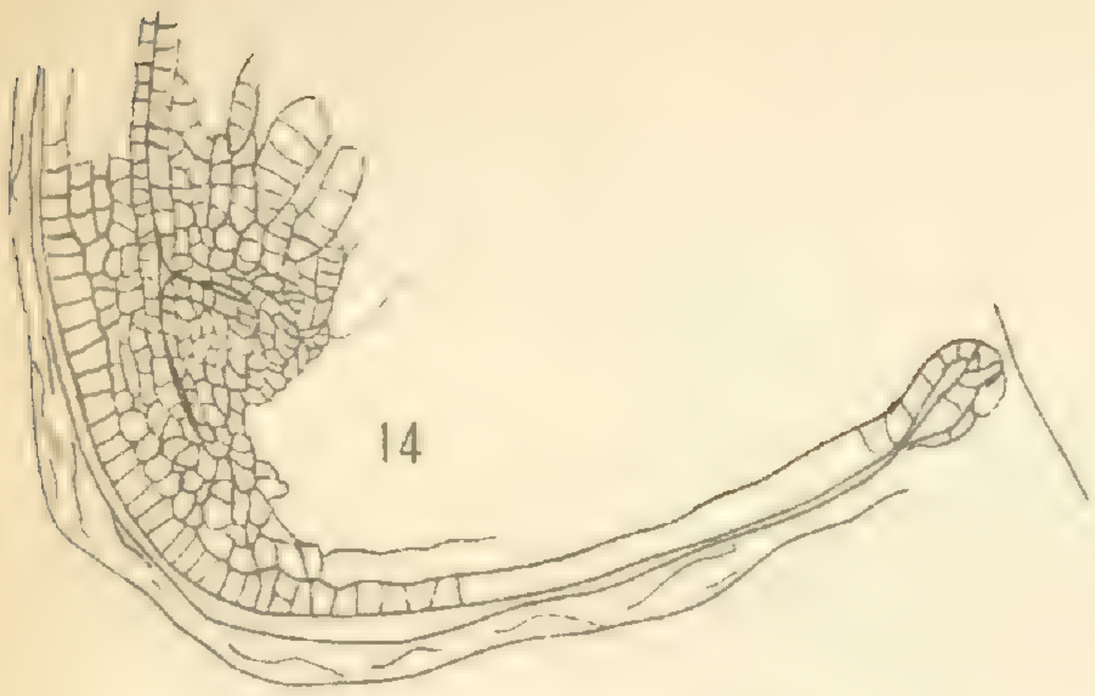
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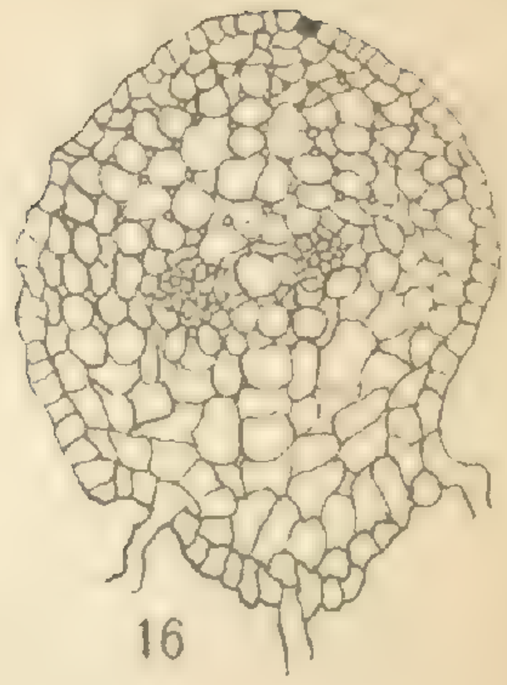
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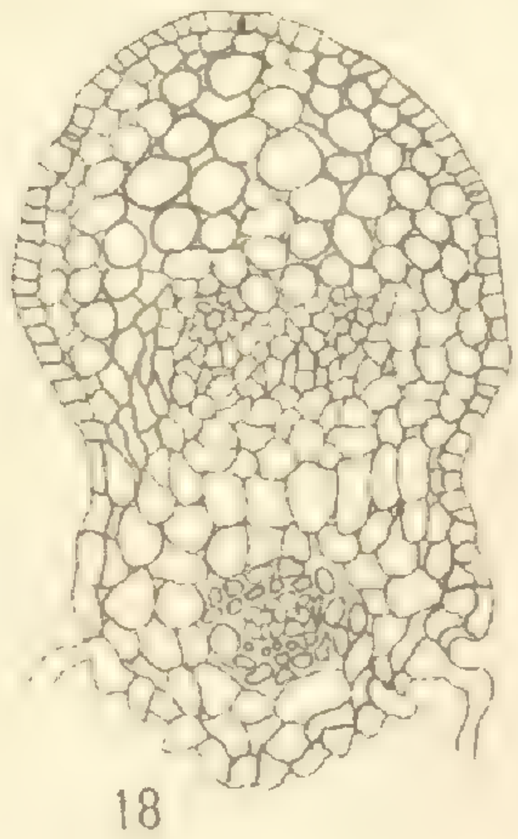
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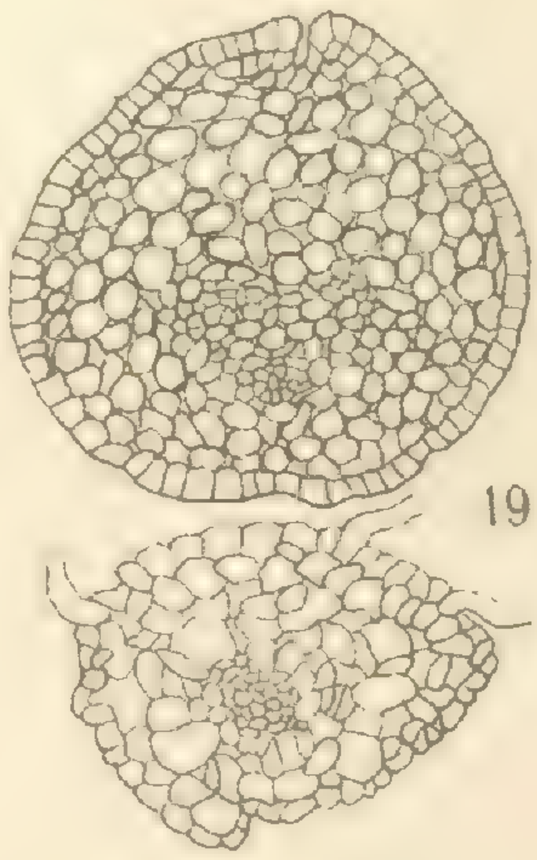
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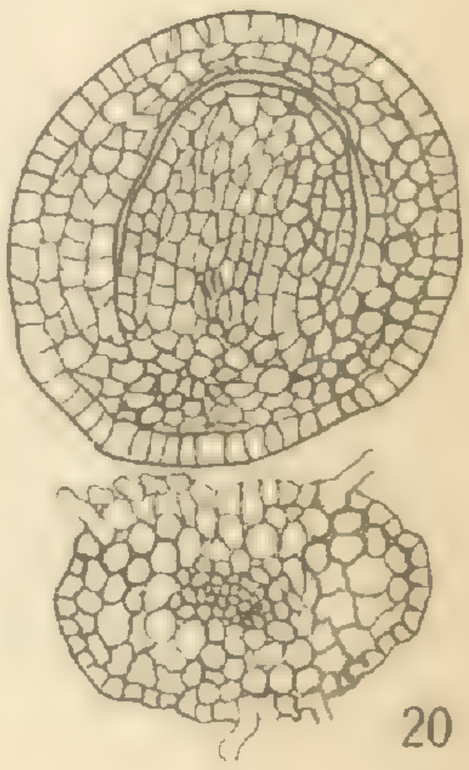
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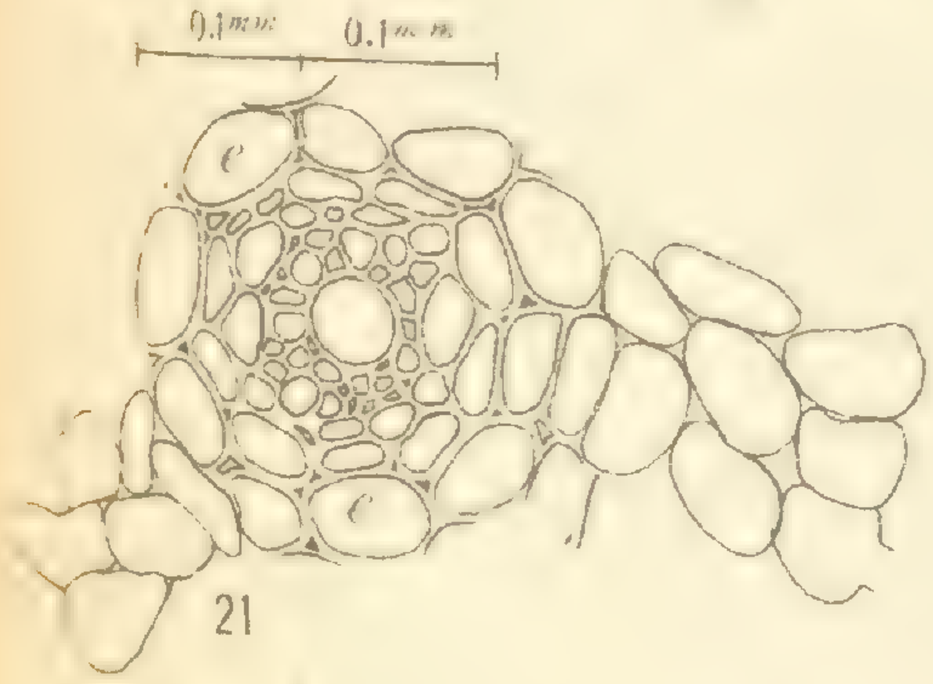

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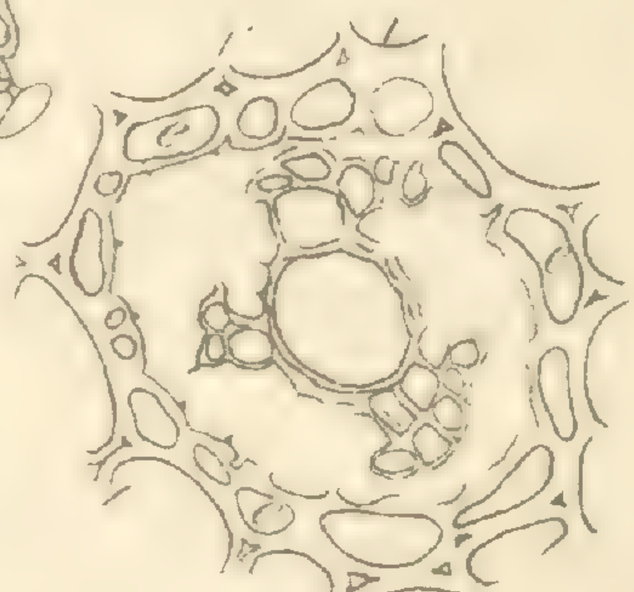

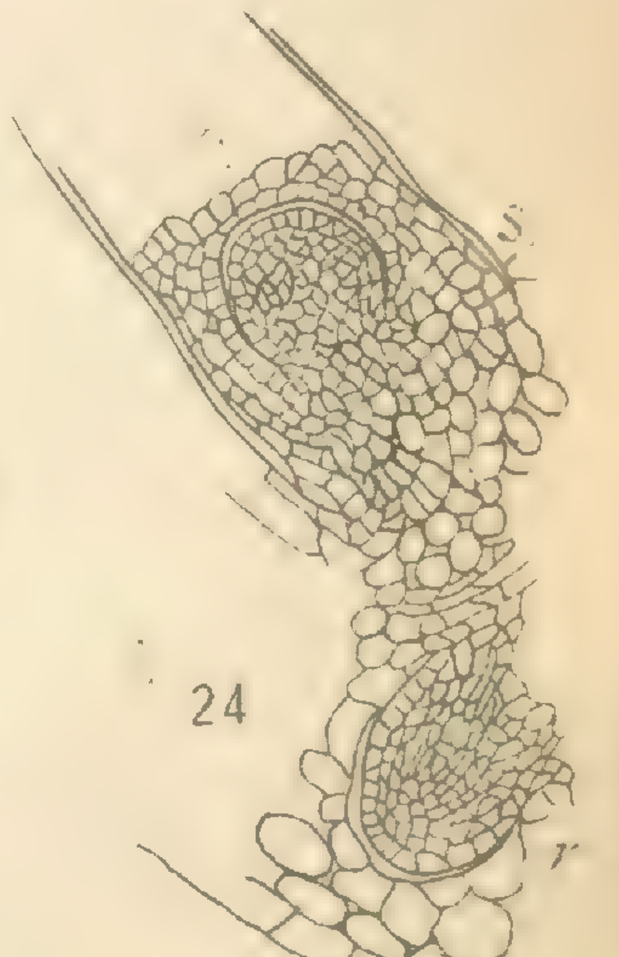

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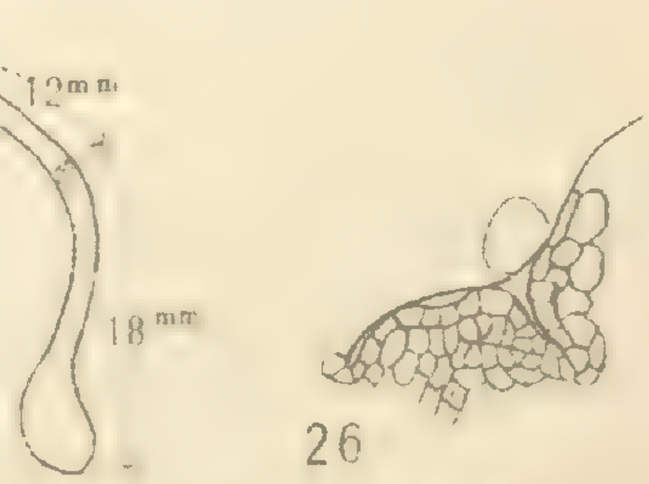
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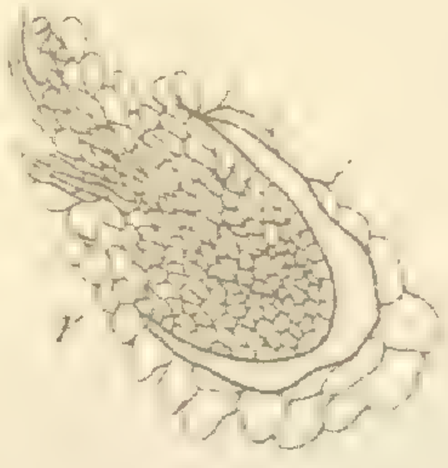

FIG. 28.—The three buds in the immature bulbs of *E. americanum;* *1*, main stem apex; *2*, bud axillary to leaf; *3*, bud axillary to scale; *1* and *3* on the same section.

FIG. 28*a*.—Sagittal section of bud *3*, to show apical dome.

FIG. 29.—Outline of entire section shown in fig. 28; relation of buds *1* and *3*.

FIG. 30.—Similar section in reference to bud *2;* in each the sheathing base of the petiole is *p*.

FIGS. 31–33.—Cross-sections of bulb rudiment, showing relation of the same structures as shown in figs. 28–30; the sections follow in order of their numbers but are not consecutive.

FIGS. 34, 35.—Cross-sections of developing flower bud in early September and early December, on the same scale and in the same orientation; *f*, foliage leaves; *p*, petals; *s*, stamens; *o*, ovary wall; *l*, line of dehiscence (lateral margin of carpel); *w*, wing-placenta from median region of carpel; *m*, *m′*, normal and degenerating microspores.

FIG. 36.—Twin embryos of *E. americanum*, ×5; the union of the two cotyledons shown below in outline.

REVERSIONARY CHARACTERS OF TRAUMATIC OAK WOODS[1]

IRVING W. BAILEY

(WITH PLATES XI AND XII)

In studying the phylogeny of plants there are certain principles or canons of comparative anatomy which have been formulated within recent years by morphologists and anatomists. Thus the application, to seedling plants, of HAECKEL'S law of recapitulation for stages in ontogenesis has been strikingly illustrated by STRASBURGER, GOEBEL, JEFFREY, EAMES, and others. Furthermore, the persistency of ancestral characters in certain regions of plants has been well established. In this connection the researches of SOLMS-LAUBACH, SCOTT, and JEFFREY have shown conclusively that the cone axis is often the seat of primitive characters. The importance of foliar organs in connection with ancestral characters has been shown by SCOTT, JEFFREY, and FAULL. JEFFREY has further pointed out in his memoir on *Sequoia*[2] the importance of vigorous cone-bearing branches of *Sequoia gigantea* as the seat of recapitulation of ancestral conditions. The importance of hypertrophied or wounded areas as the seat of reversion to primitive characters is strongly appreciated by zoologists. This principle has also been applied to the traumatic areas of plants by JEFFREY, who has pointed out the traumatic reversionary origin of resin canals in the wood of the higher Abietineae,[3] certain Sequoiineae,[4] and the older Araucarineae,[5] which normally possess none of these

[1] Contributions from the Phanerogamic Laboratories of Harvard University, no. 24.

[2] The comparative anatomy and phylogeny of the Coniferales. I. The genus *Sequoia*. Mem. Boston Soc. Nat. Hist. **5**:441–459. *pls. 68–71*. 1903.

[3] The comparative anatomy and phylogeny of the Coniferales. II. The Abietineae. Mem. Boston Soc. Nat. Hist. **6**:1–37. *pls. 1–7*. 1904.

[4] The comparative anatomy and phylogeny of the Coniferales. I. The genus *Sequoia*. Mem. Boston Soc. Nat. Hist. **5**:441–459. *pls. 68–71*. 1903.

[5] The wound reactions of *Brachyphyllum*. Annals of Botany **20**:383–394. *pls. 27, 28*. 1906.

Araucariopitys, a new genus of araucarians. BOT. GAZETTE **44**:435–444. *pls. 28–30*. 1907.

structures; and has demonstrated the presence of traumatic marginal tracheids in the wounded wood of *Cunninghamia sinensis*.[6]

An interesting parallel to the work of JEFFREY upon traumatic reversions in the Coniferales has been noted by the writer in the traumatic reversions of wounded oak wood. Owing to the controversy which exists as to the relative primitiveness of the Abietineae and Cupressineae this occurrence of traumatic reversions in a dicotyledonous genus is of particular interest in demonstrating the application of the principles of experimental morphology to plants.

Before describing the reversionary characters of oaks, it will be well to have clearly in mind the normal structure of the wood of existing oaks, and also that of ancestral types. As is well known, the secondary xylem of living oaks consists of vessels, fibers, tracheids, and parenchyma. The last occurs vertically as wood parenchyma, and horizontally disposed in plates of tissue extending radially, the so-called primary and secondary medullary rays. The "primary rays" (fig. 1) are the distinctive feature of oak wood, the "silver grain," and are broad, fusiform masses, many cells in width, which are supposed to originate as inclusions of fundamental tissue between the primary fibrovascular bundles. The "secondary rays" are thin sheets of tissue, and consist of a single row of cells when seen in tangential or transverse section (fig. 1). These rays, unlike the primary rays, are supposed to originate only with secondary growth.

In contrast to this type of structure occurring in the mature wood of extant oaks, EAMES has shown[7] that certain miocene oaks do not possess large rays composed of homogeneous masses of ray parenchyma, but have in their place bands of aggregated smaller rays which are separated by fibers and wood parenchyma. These rays are homologous with the "false rays" of the Betulaceae, and lead to the conclusion that the so-called primary rays of extant oaks have been built up by an aggregation and fusion of numerous originally uniseriate rays.

[6] Traumatic ray tracheids in *Cunninghamia sinensis*. Annals of Botany **22**:593–602. *pl. 31*. 1908.

[7] On the origin of the broad ray in *Quercus*. BOT. GAZETTE **49**:161–166. *pls. 8, 9*. 1910.

The writer has shown,[8] by a study of numerous species of Betulaceae and Fagaceae, that ample evidence of a compounding process exists in the rays of many living oaks, alders, birches, and hornbeams. Thus many American live oaks (fig. 5) possess bands of aggregated rays which are similar to the false rays of the Betulaceae. Among alders and birches species may be found with non-aggregated uniseriate rays, aggregated small rays, and large homogeneous rays like the so-called primary rays of oak. In fact, in the genus *Alnus* species may be found which form a perfect series of transitional steps between alders with non-aggregated uniseriate rays and *Alnus rhombifolia* Nutt., which often possesses large compound rays such as are found in the higher oaks.

Further, EAMES has shown that in the development of seedling oaks a similar series of stages occur. Thus in seedlings of *Quercus alba* L. and *Q. rubra* L., which in the adult possess broad homogeneous rays, the first-formed wood resembles the adult wood of chestnut in possessing non-aggregated uniseriate rays. In the further growth of the young plant, aggregations of rays develop, which by subsequent fusion constitute the large rays of the mature wood.

Thus three lines of evidence, afforded by the study of seedling stages, fossil ancestral forms, and the development of ray structures in living forms, show conclusively that the wood of primitive Fagaceae and Betulaceae was characterized by the entire absence of large medullary rays. With the development of unequal seasonal temperatures, a highly organized storage system for foods became advantageous to plants, and the large rays of modern oaks have been evolved by an aggregation and fusion of numerous uniseriate rays to meet this demand.

With these preliminary statements on the normal and ancestral features of oak wood, we may now turn to a more detailed consideration of the abnormal structures which exist in traumatic oaks. It has been pointed out above that traumatic regions are often the seat of ancestral characters and show a series of stages similar

[8] Relation of the leaf trace to the origin and development of compound rays in the dicotyledons. Annals of Botany. *In ed.*

to embryonic or seedling stages. We should accordingly expect to find in wounded oak wood a reversion to primitive ray structure. That this reversion does occur has been shown conclusively by the examination of numerous areas of wounded oak wood. In fact, in all cases a complete series of transitional stages in the development of compound rays occurred, resembling the series of steps found by EAMES in the development of seedling plants. The wood formed immediately after wounding possesses characteristically only uniseriate rays. In following layers aggregations of the rays develop, with subsequent enlargement of the uniseriate rays, and their subsequent fusion into homogeneous masses or compound rays. During this compounding process, fibers and wood parenchyma included in the fusing mass are transformed into ray parenchyma.

In all cases, in securing material, burls and distorted tissues were carefully avoided and straight-grained traumatic tissue selected.

In fig. 1 may be seen a tangential section of the normal adult wood of *Quercus nigra* L. The so-called primary and secondary rays are characteristically developed; the former consists of a homogeneous mass of ray parenchyma. In contrast to this the traumatic wood of the same species may be seen in fig. 2. The large ray is seen to consist of a compounding mass of smaller rays.

Figs. 3 and 4 illustrate the normal and traumatic condition in *Quercus virginiana* Mill., the important live oak of the southern United States. As may be seen, in this species the normal adult wood is characterized by an imperfectly compounded ray. Numerous included fibers and wood parenchyma cells, evidences of fusion, are usually present. Fig. 4 illustrates the reversion of the wood in the vicinity of the wound to the non-aggregated uniseriate condition.

In figs. 5 and 6 are shown sections of the normal and the traumatic wood of *Quercus densiflora* Hook. and Arn., a live oak whose normal adult wood is characterized by large rays in which the process of compounding is clearly shown. The wounded wood of the species reverts to a more primitive type of compounding, as may be seen in fig. 6.

Figs. 7–10 illustrate the normal and traumatic wood of the well known *Quercus alba*, a deciduous oak with highly specialized ray structure. Figs. 8 and 10, tangential and transverse sections respectively of the traumatic wood, show that this species also reverts to ancestral type of ray structures.

This reversion to ancestral conditions has been found by the writer in woody tissues subsequent to severe injury. Slight injuries, on the other hand, particularly in oaks with highly specialized ray structure, often produce no morphological effect upon the wood. In a limited number of cases very slight wounds have produced a stimulation of the compounding tendency or acceleration of development rather than a reversion to ancestral structures. In fig. 11 may be seen a cross-section of *Alnus* sp. The lower portion of the figure shows none of the so-called false rays, but in the upper half numerous rays have developed abruptly outside a zone indicating slight injury. Fig. 12 shows a similar phenomenon in the young stem of *Quercus densiflora*. In the lower half may be seen normal seedling wood in which only uniseriate rays occur. Starting from a zone of slight injury in the middle of the section, a compound ray has suddenly appeared in the upper portion of the figure. From this we see that very slight injuries produce an acceleration in the formation of compound rays.

SUMMARY AND CONCLUSIONS

1. The phylogenetic importance of traumatic areas as the seat of reversion to primitive structures is well illustrated by the specimens of wounded oak wood which have been examined by the writer.

2. In traumatic wood progressive stages are found which are similar to the stages of recapitulation found in the seedling, and equivalents to the condition found in adult miocene oaks.

3. Woody tissues in the immediate vicinity of a severe wound show only non-aggregated uniseriate or small rays. In subsequently formed tissues the gradual building up of the compound ray may be traced in a consecutive series of steps to the normal homogeneous large ray of the adult wood.

4. On the basis of traumatic and developmental as well as paleo-

botanical evidence, the large homogeneous masses of ray parenchyma, or the so-called primary rays of oaks with deciduous foliage, appear to have been built up by an aggregation and fusion of numerous uniseriate rays.

5. Traumatic reversions are confined to regions which have been severely injured. Occasionally areas where the traumatic effect has been slight show an acceleration of the compounding process instead of a reversion to ancestral stages.

6. The so-called primary ray is seen to have originated from an aggregation and fusion of secondary rays, and to be in no way related to inclusions of fundamental tissue between the primary fibrovascular bundles. From this phylogenetic relation of the two sorts of medullary rays it seems that the term primary is inadmissible entirely for the large rays of oak, and that the term *compound* might be advantageously substituted.

In conclusion I wish to express my sincere thanks to Mr. G. B. SUDWORTH, dendrologist of the U.S. Forest Service, for material of *Alnus rhombifolia*. I am also much indebted to Professor E. C. JEFFREY for suggestions and advice, and to Mr. A. J. EAMES for material of several wounded oaks.

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EXPLANATION OF PLATES XI AND XII

PLATE XI

FIG. 1.—*Quercus nigra:* tangential section of the normal adult wood, showing the so-called primary and secondary rays; the former are seen to consist of large masses of homogeneous ray parenchyma; ×120.

FIG. 2.—*Quercus nigra:* tangential section of the traumatic wood, showing compounding mass of small rays; ×120.

FIG. 3.—*Quercus virginiana:* tangential section of the normal adult wood, showing strong evidences of a compounding process; inclusions of fibers and wood parenchyma cells occur conspicuously; ×120.

FIG. 4.—*Quercus virginiana:* tangential section of the traumatic wood, showing uniseriate non-aggregated rays in the immediate vicinity of a severe wound; ×120.

FIG. 5.—*Quercus densiflora:* tangential section of the normal adult wood, showing aggregating and fusing mass of small rays; ×60.

FIG. 6.—*Quercus densiflora:* tangential section of the traumatic wood, showing aggregation of uniseriate and biseriate rays; ×120.

PLATE XII

FIG. 7.—*Quercus alba:* tangential section of the normal adult wood, showing highly organized broad homogeneous ray; ×120.

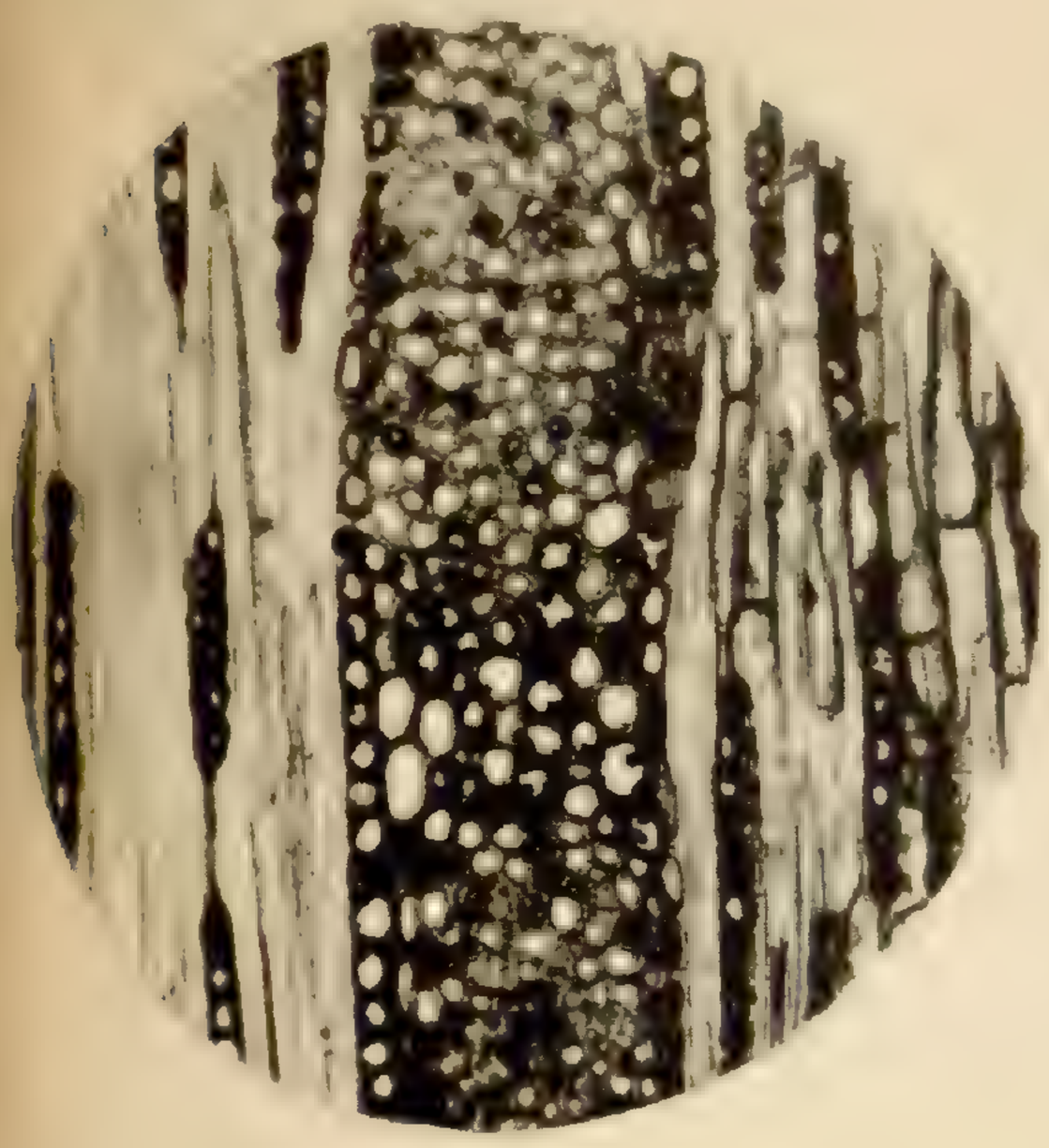
FIG. 8.—*Quercus alba:* tangential section of the traumatic wood, showing the aggregation and fusion of triseriate and biseriate rays; these rays have been produced by the enlargement or growth in diameter of uniseriate rays; ×120.

FIG. 9.—*Quercus alba:* transverse section of the normal adult wood, showing the highly organized type of ray; ×120.

FIG. 10.—*Quercus alba:* transverse section of the traumatic wood, showing aggregation of uniseriate, biseriate, and triseriate rays; ×120.

FIG. 11.—*Alnus* sp.: transverse section of very slightly injured wood; compounding rays are absent from the lower half of the section; starting abruptly from a line of slightly injured tissue which crosses the middle of the section, numerous rays extend outward to the exterior of the stem; ×40.

FIG. 12.—*Quercus densiflora:* transverse section of very slightly injured wood; the lower half of the section possesses only uniseriate rays, but starting from the middle of the section a compounding ray has originated from a slight injury to the wood; ×60.



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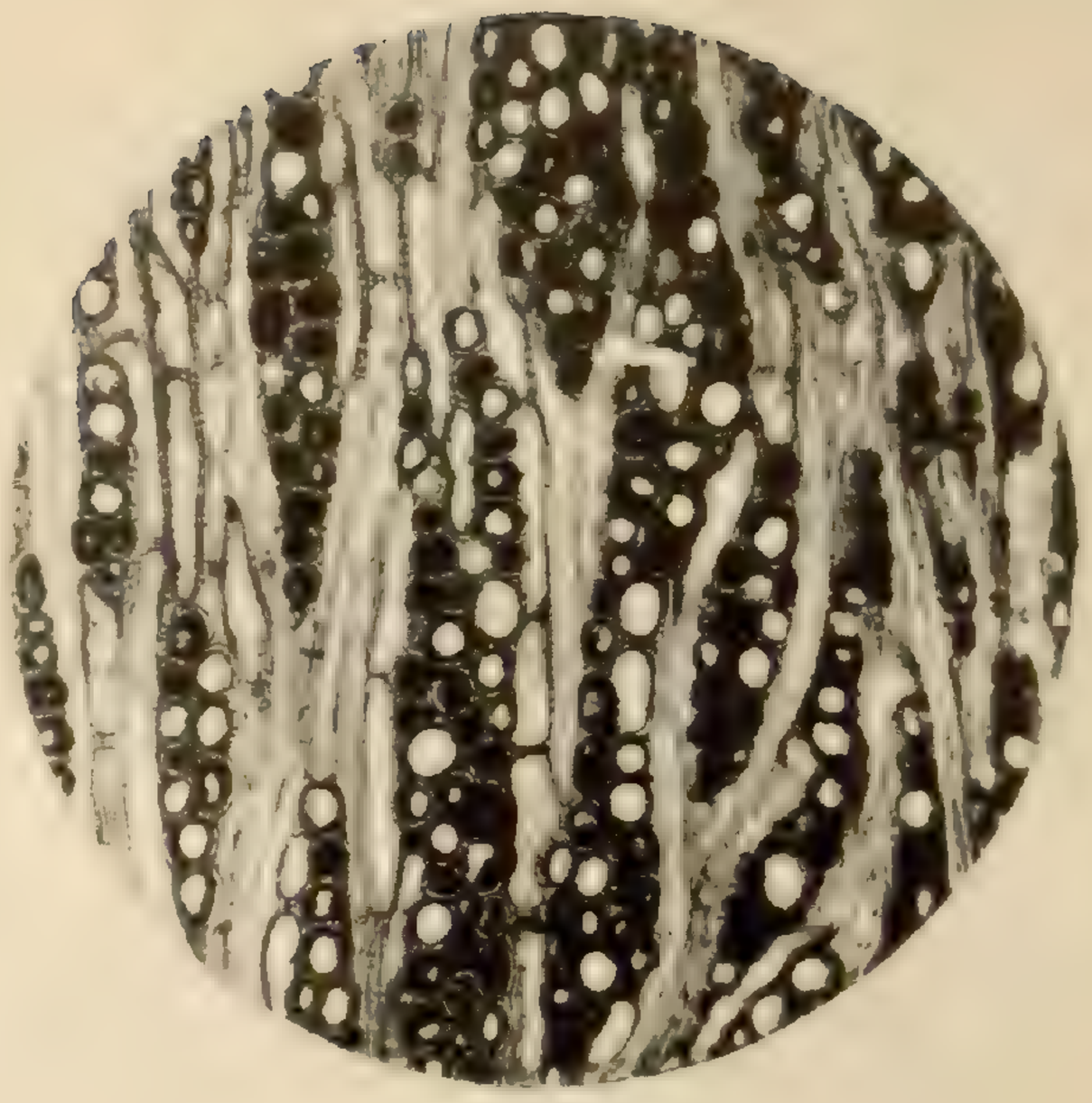

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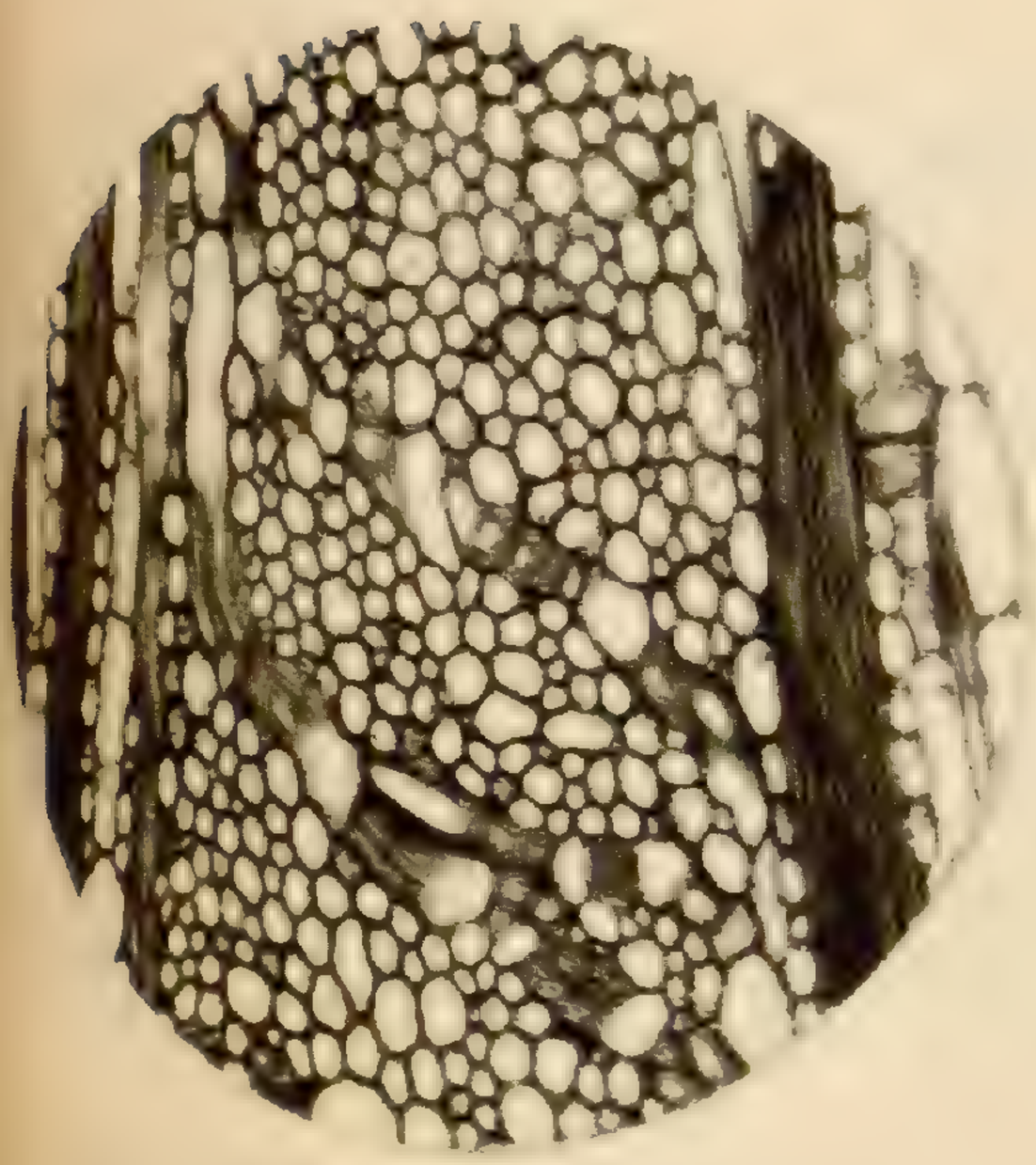

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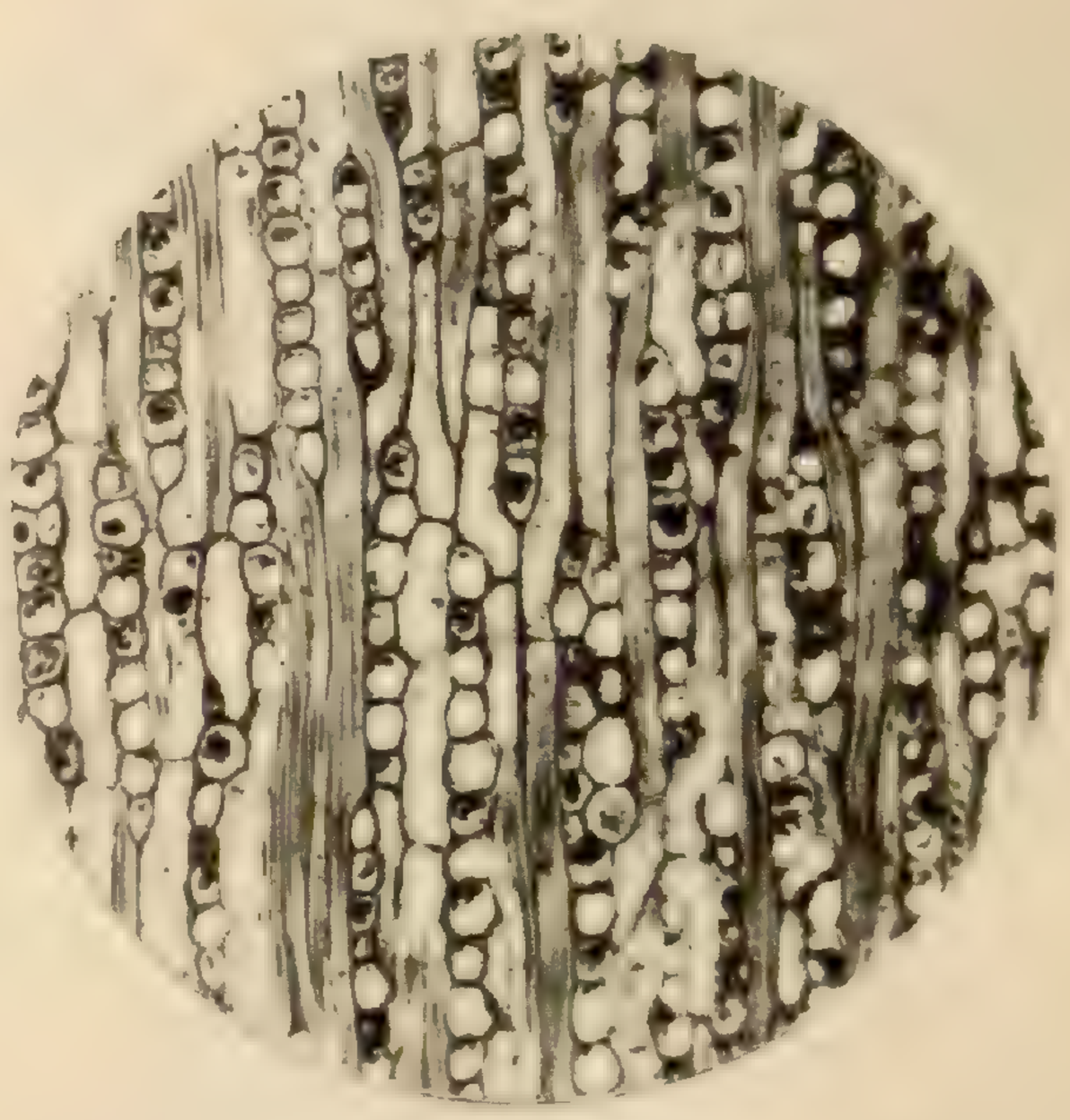

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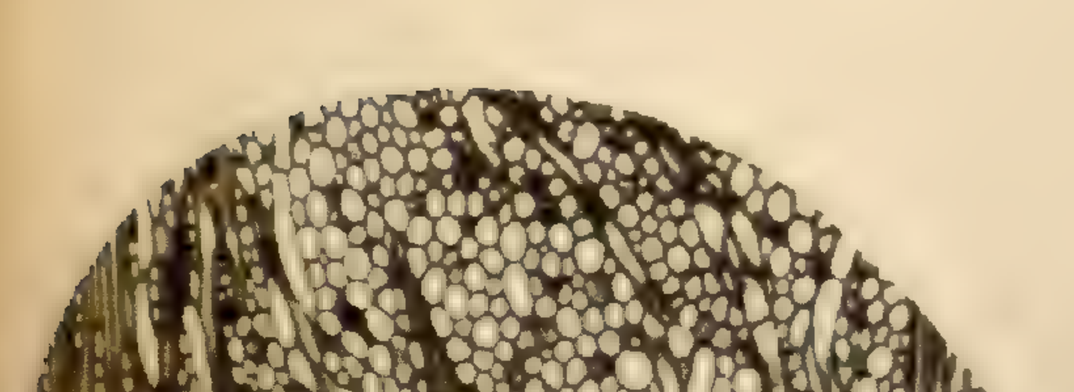

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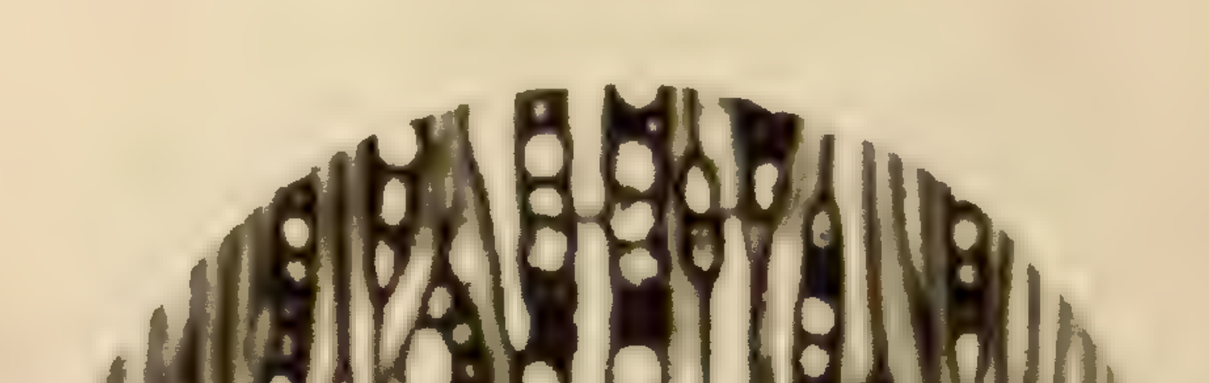

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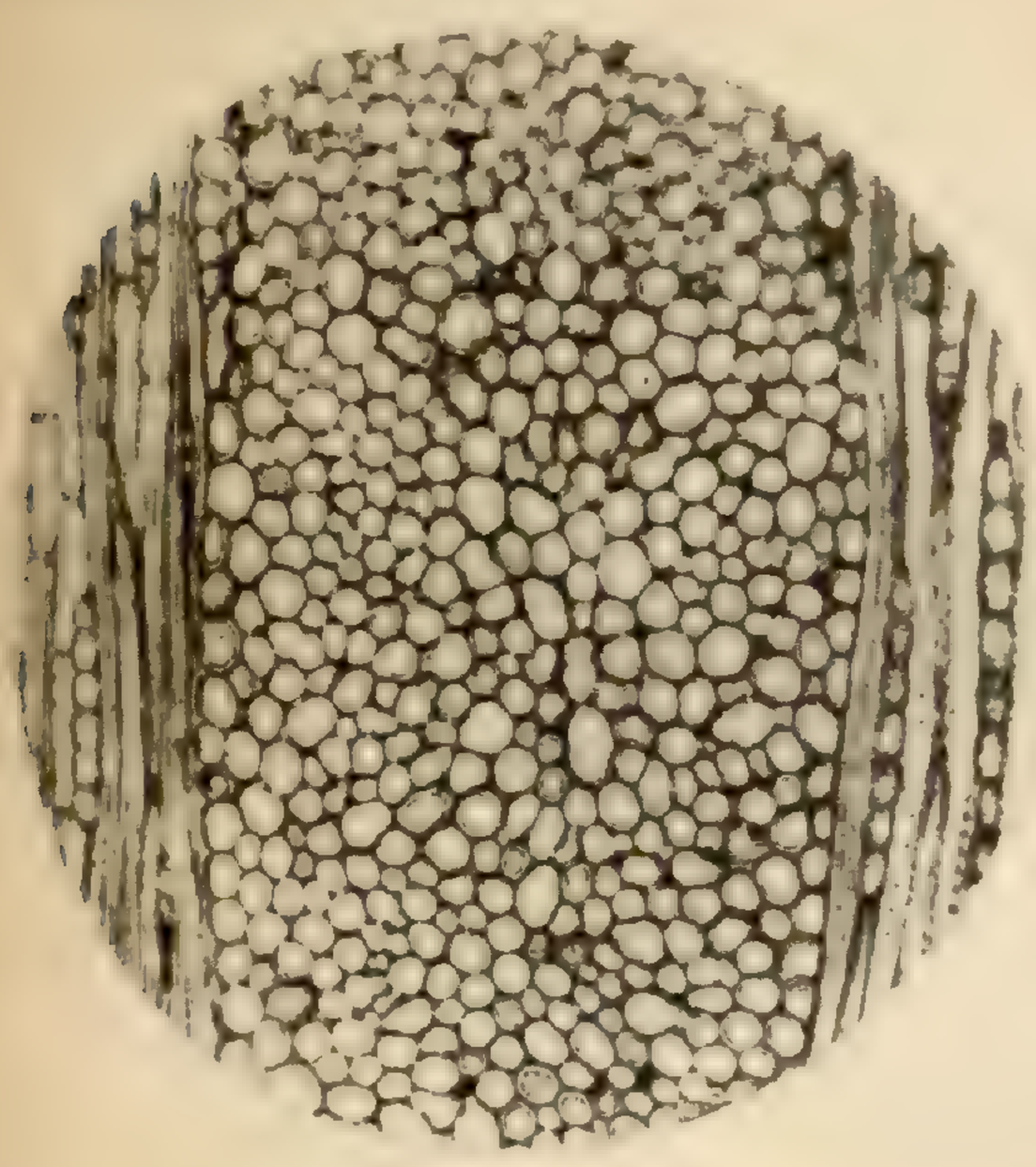

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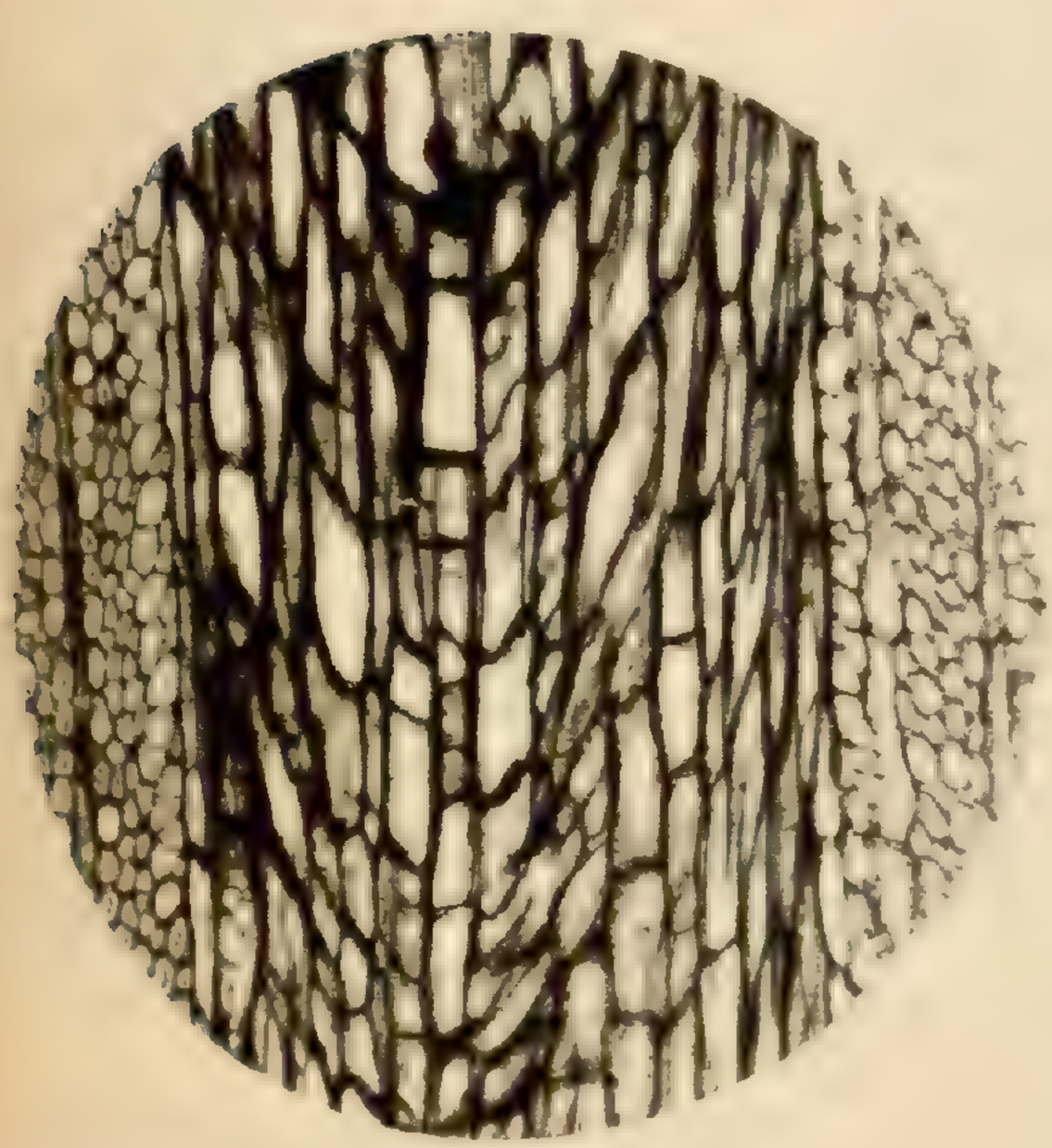

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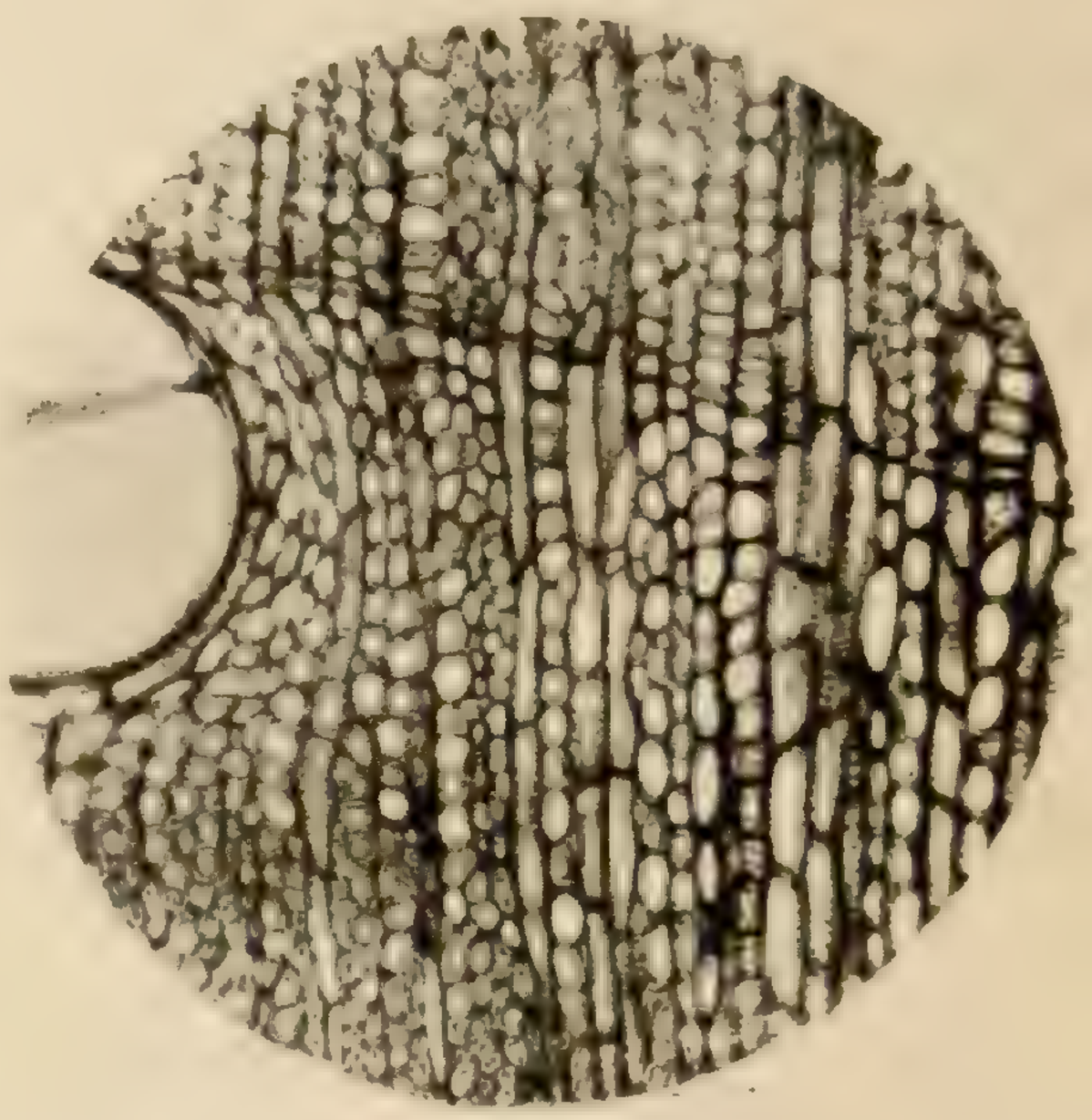

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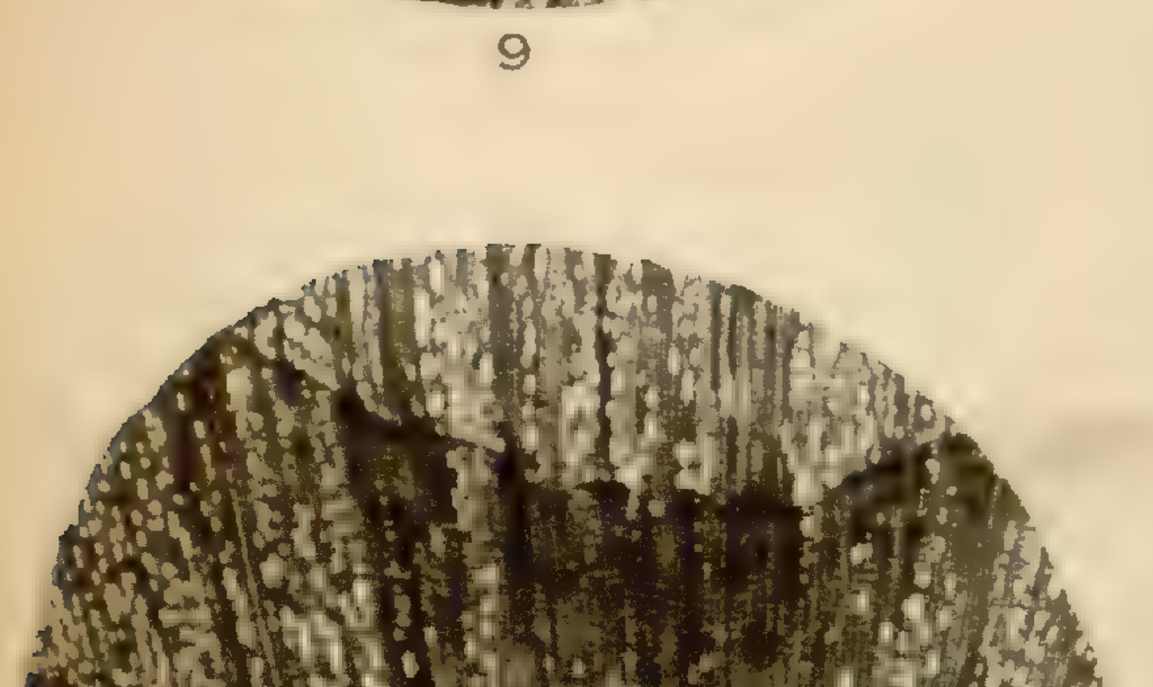

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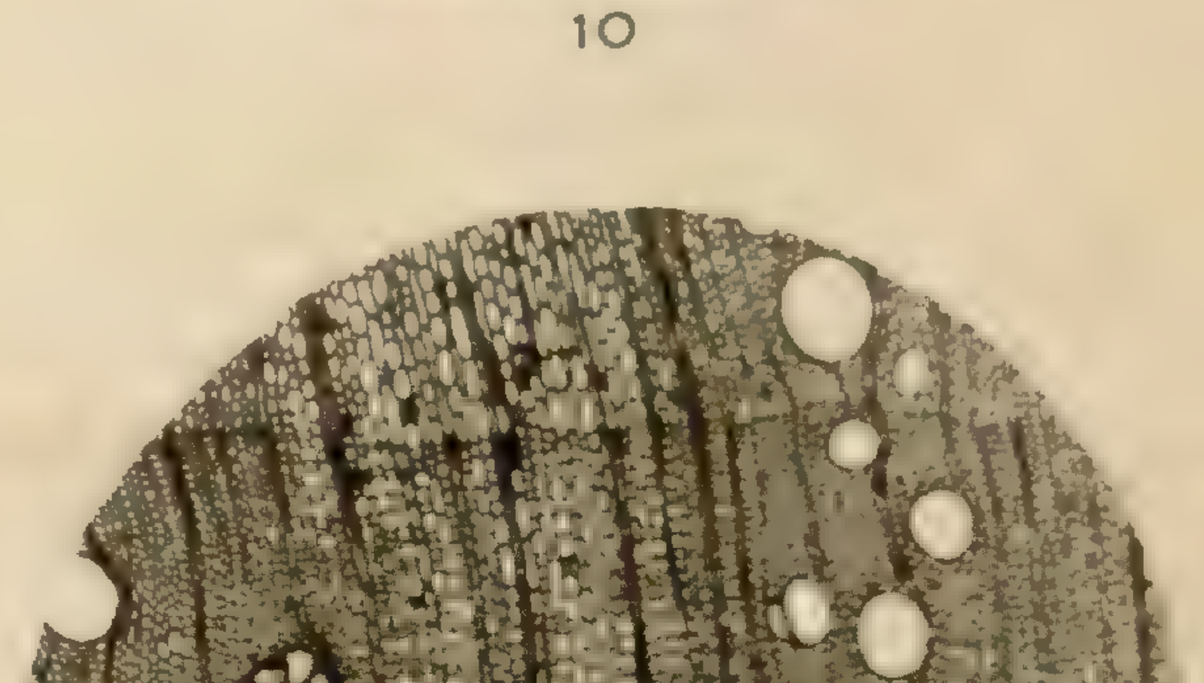


12

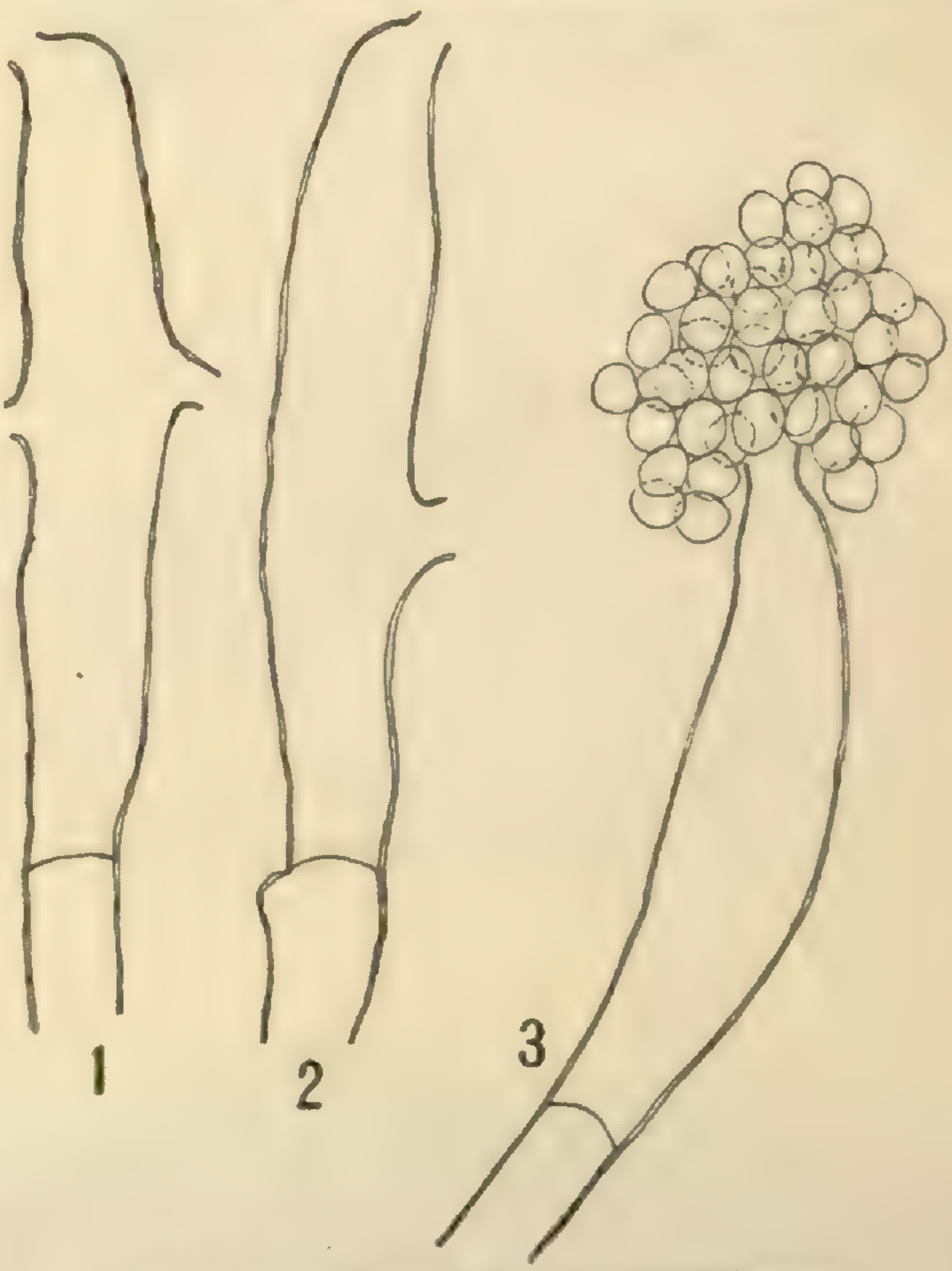
BRIEFER ARTICLES

ANOTHER NEW ACHLYA

(WITH EIGHT FIGURES)

In the fall of 1909 a species of *Achlya* that was found to be new appeared in cultures from pools around Chapel Hill, N.C. It was separated from other forms and has now been kept under observation in pure cultures for nearly a year. It adds one more to the *Racemosa* group proposed by me in 1908.[1] The species may be described as follows:

Achlya caroliniana, sp. nov.—Hyphae rather stout, about 48 μ at the base and 20 μ near the tip, in strong cultures reaching a length of 1.5 cm. Zoosporangia irregularly cylindric, about 20–30 μ in diameter, often discharging by several openings. Oogonia abundant, spherical, smooth, and unpitted; terminating short, slender branches, which are racemosely borne on the strong main hyphae. Oogonial branches generally simple, but often giving off one or two branches near the base which also terminate in oogonia, and, as a rule, are curved downward. Oospores generally 1 or 2, often 3, and very rarely 4 or 6 (8 were seen twice). They are centric, with a diameter varying from 18.5 to 26 μ, averaging about 22 μ. Antheridia absent, but hypogynous antheridial tubes often appear through the basal partition exactly as in *Achlya hypogyna* Coker.



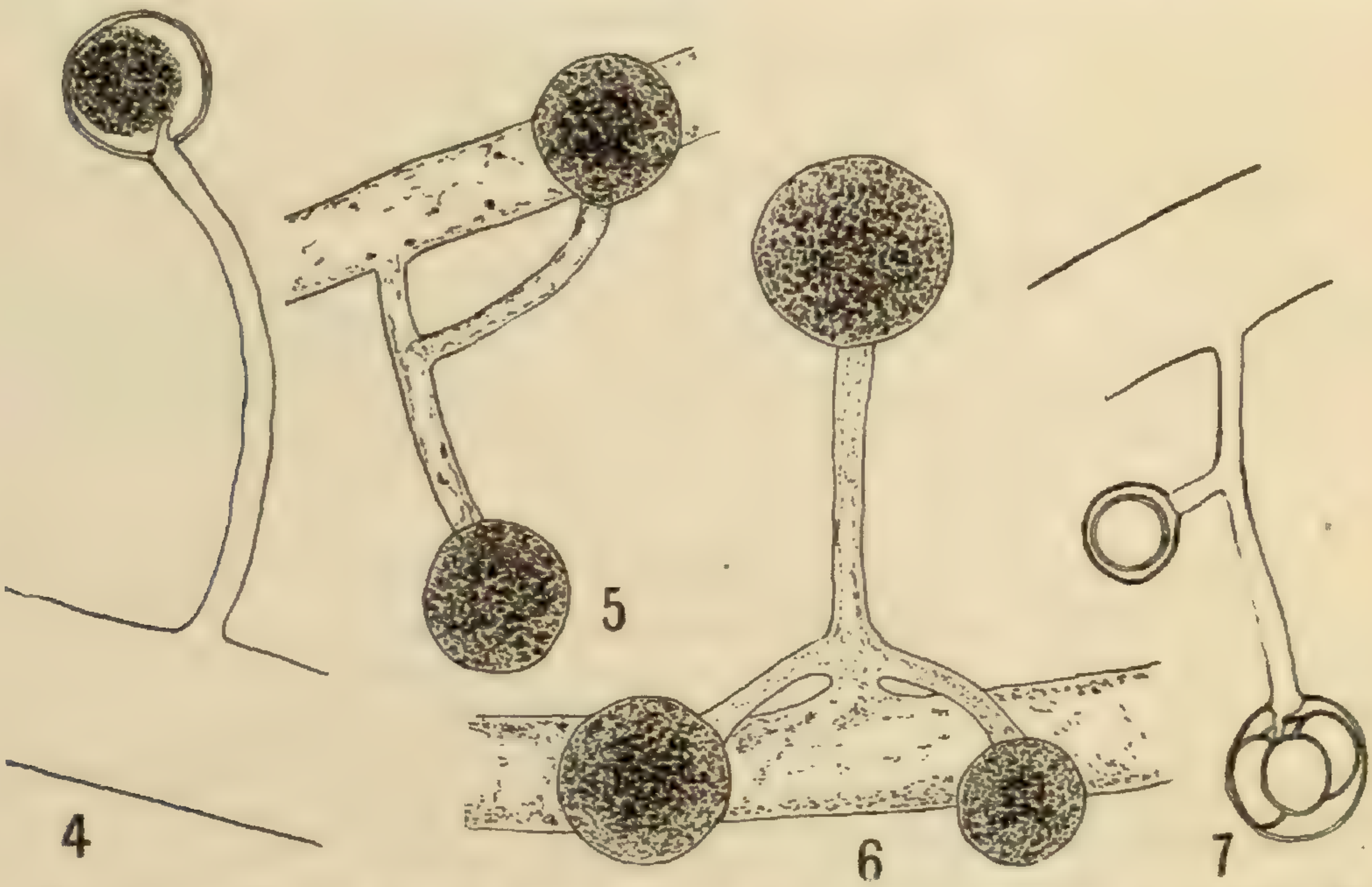
FIGS. 1–3.—Sporangia of various forms; all ×335.

Typical zoosporangia are shown in figs. 1–3. In cultures that have become somewhat foul, the spores may be fully formed, but not discharged. In several such cases the spores

[1] A new species of Achlya. BOT. GAZETTE 45: 194, 195. 1908.

were seen sprouting and sending their tubes through the sporangium wall, as is normally the case in *Alpanes*.

Figs. 4–7 represent the normal arrangement of the oogonia; the hypogynal tube will be noticed in fig. 4. In countings from my cultures,



FIGS. 4–7.—Fig. 4, simple oogonial branch terminating in an oogonium; fig. 5, oogonial filament with one branch; fig. 6, same with two branches; fig. 7, a branched oogonial filament with terminal oogonium containing four oospores; all ×335.

this tube was present only in about one-sixth of the oogonia, but it appears in all cultures and is one of the most distinctive characters of the species. The appearance of an antheridial tube, not from an antheridium, but from the vegetative coenocyte, is a most singular occurrence, and would seem to be a degenerate condition induced by the suppression of fertilization. I could find no evidence of fertilization even in cases where a tube was found. In not a single case was an antheridium seen below the oogonium.

FIG. 8.—Exceptional oogonium with two projections on surface; ×335.

The arrangement shown in fig. 6, suggesting the three balls of a pawnbroker's shop, occurs so often and is so striking as to be one of the best diagnostic characters of the species. The lower branches are typically recurved (figs. 5, 6), but not always (fig. 7).

Out of many thousands of oogonia seen, a very few had one or two short rounded outgrowths from

the surface (fig. 8) like those that are characteristic of *A. hypogyna*. In only two cases were intercalary oogonia seen.

In old cultures the protoplasm becomes condensed and segregated into certain restricted areas of the hyphae to form resting fragments, which, though not of definite shape, may be regarded as chlamydospores.

In the *Racemosa* group, as mentioned above, there may now be included *A. racemosa*, *A. racemosa* var. *stelligera*, *A. hypogyna*, and *A. caroliniana*. The group may be defined as follows:

Oogonia terminating short branches, racemosely arranged. Oospores few, generally one or two. Antheridia absent, or of suboogonial origin.—W. C. COKER, *Chapel Hill, N.C.*

SOME NEW SAPROPHYTIC FUNGI OF THE MIDDLE ROCKY MOUNTAIN REGION

Until a year ago (June 1909) the saprophytic fungi of the Rocky Mountain region included within Wyoming had remained practically untouched. It was with great interest, therefore, that the writer began the task of making a collection of these fungi under the kindly suggestion and help of Professor AVEN NELSON. The particular region studied includes the whole of the Medicine Bow National Forest, together with the vast extent of the Laramie Plains. The timber in the forest is chiefly lodgepole pine, Englemann spruce, Douglas fir, and balsam, with dense growths of aspen on the boundaries. In many places the timber is very dense, in consequence of which the humus formed of the needles is very thick; the soil in the open timber also is very rich. The whole region is well watered by the melting snows and by the numerous mountain streams and creeks, resulting in very favorable conditions for the growth of the fleshy fungi. The great difference in the altitude, which ranges from 2130 to 3900 meters, further aids in the formation of many varying conditions, thus giving not only richness in specimens but a wealth of species as well.

In the very precursory examination of the region, the writer was astonished at the great quantity and variety of forms. The further collections, which it is expected will be made, will no doubt extend the list greatly. This list, as finally worked out, will be published as a whole, but for the present the following apparently new species only are presented.

Catathelasma, gen. nov.—Pileus somewhat fleshy, convex, then expanded: lamellae very decurrent, somewhat unequal, with acute edges:

stipe furnished with a ring and of the same substance as the pileus: volva large, white, with a thick margin: spores white.

The ring and volva, together with the very decided decurrent gills (upon which character the generic name is based), are telling characteristics of this genus of the Leucosporae.

C. evanescens, sp. nov.—Pileus 13 cm. broad, white, deep cream in center, broadly convex to nearly plane, smooth, damp, broadly elliptical in outline; margin entire: flesh whitish, compact, thick in center, thinner near margin: lamellae very decurrent, short ones intermixed with long ones, white, 2–3 cm. wide near margin of pileus, becoming narrowed near and on stipe, subdistant, edges acute: stipe very short, thick, 1 cm. long, 4 cm. thick, fleshy, hollow, smooth, white; annulus delicate, evanescent, situated on stipe just below gills: volva large, white, smooth, opening around top leaving a thick even white margin, persistent and closely embracing base of stipe: base large, white, bulbous: spores white, smooth, elliptic to fusiform, 14–17.5×3–5 μ.—Whole plant when dried becomes a rich ochre with reddish tinge.

Habitat: Open balsam and spruce woods, occurring singly in sod on thick humus; Brooklyn Lake, Wyoming, Snowy Range, alt. 3500 meters, September 8, 1909, no. 88.

Clitocybe pruinosa, sp. nov.—Pileus 3.5 cm. wide, plano-convex to slightly depressed, rich reddish brown over salmon, paler at margin, dry, smooth, shining: margin turned down and entire: flesh compact, white, tinged with color of cap: lamellae thin, narrowing behind, salmon yellow, close, very decurrent, becoming somewhat powdered with numerous white spores: stipe fleshy, 5 cm. long, 1 cm. wide, concolorous but lighter than cap, hollow, smooth: spores white, spiny, globose, 7–10.5 μ.

Habitat: Pine humus, open pine woods; Foxpark, Wyoming, August 14, 1909, no. 83.

COLLYBIA MACULATA **moschata,** var. nov.—Pileus fleshy, firm, 6 cm. wide, convex to nearly plane, white, glabrous, shining, becoming tinged or stained with pinkish red blotches, disk sometimes broken up into large polygonal plates; margin turned down and even; flesh white, compact, tinged with pink just beneath the surface: lamellae whitish, in one specimen a faint pink tinge, adnexed to nearly free: stipe stout, firm: 3 cm. long, 2 cm. wide, swollen in middle, stuffed, becoming hollow, curved, narrowed at base, striate, slightly roughened by broken fibers, spores white, smooth, sometimes with a slight point at one end, 7×4 μ.—It has a strong, almost overpowering odor of musk.

Habitat: On side of dead lodgepole pine log, clustered; Foxpark, Wyoming, alt. 2900 meters, August 13, 1909, no. 79.

Entoloma viridans, sp. nov.—Pileus 3.5–5.5 cm. broad, fleshy, broadly convex, hygrophanous when moist, gray, margin tinged with rose pink and disk becoming dull green, or the coloring may be reversed, the disk rose pink and margin a dull green, when dry the whole plant becomes silky shining: flesh white, becoming dull when dry: margin turned down, entire, smooth: lamellae all even, light pinkish yellow, becoming a salmon pink color, 2 mm. broad, slightly sinuate, adnate then separating, interspaces venose: stipe fleshy, white, pruinate, hollow, round, quite bulbous at base, attenuating upward, 4.5 cm. long, 1.5 cm. wide: spores coarsely warted, pink, 7×10 μ.

Habitat: Damp humus; Brooklyn Lake, Wyoming, alt. 3500 meters, bank of Nash's Fork, September 3, 1909, no. 119.

Gloeophyllum ferrugineum, sp. nov.—Pileus hard, corky to woody, oblong-dimidiate to flabelliform, 1–2×2–12×1–1.5 cm.; surface azonate, strigose-tomentose, scrupose, dark ferruginous to umbrinous; margin rather thick, sterile, tomentose, bright ferruginous: context corky, homogeneous, bright ferruginous, indistinctly zoned, about 7 mm. thick; tubes lamelloid, quite decurrent, tomentose, ferruginous but paler than margin of pileus, light grayish within, 1–2 mm. broad, 2–5 mm. deep; edges somewhat thin, tomentose, undulate; tubes lamelloid from the first: spores globose-ellipsoid, smooth, hyaline, 10–14×7 μ.

Habitat: On dead lodgepole pine and aspen; Cooper Creek, Wyoming, alt. 2800 meters, June 22, 1909, no. 11.

Clavaria truncata, sp. nov.—Pileate tops bright red, shading into reddish orange at top of stipe to dull flesh color at its base: ends truncate, convex to plane to somewhat concave, 0.5–3 cm. broad, smooth: whole plant to within a few centimeters of base of stipe covered with a white bloom, persisting in dried specimens: flesh creamy, spongy: stipe longitudinally grooved to base, 3–10 cm. long: spores white, 14×7 μ.

Habitat: Humus soil under balsam and spruce trees; gregarious and cespitose, 4–6 in a group; Foxpark, alt. 2900 meters, August 8, 1909, no. 66.

A plant similar to this is described by FRIES as *Craterellus pistillaris*, and by others as possibly a variety of *Clavaria pistillaris*, but in a collection of twenty specimens found in entirely different localities not one out of the number was found to have either the color or the form of typical *Clavaria pistillaris*.

RUTH HARRISON LOVEJOY, *University of Wyoming, Laramie.*

CURRENT LITERATURE

BOOK REVIEWS

The root-fungi of orchids

BURGEFF[1] has brought together the extended results of his own research and those of other students upon the root-fungi of orchids. The volume contains a comprehensive citation of literature, several tables summarizing results of experiments, and discussions of the theory of the mycorhiza question. By way of introduction, BURGEFF defines his use of the word symbiosis as that relation of two symbionts in which one aids the other in any way, if only to make existence possible under conditions otherwise impossible. After union, the two organisms form a new organism, a unit, which takes up the struggle for existence under new conditions, each being a body member. Such is claimed to be the condition of the orchids and their root-fungi. The two sections of the work are as follows:

1. *The study of the fungus independent of the plant.*—On a culture medium of agar and rain water with a slight trace of starch, 29 root-fungi, aseptically obtained from native and tropical orchids, were grown (holosaprophytic ones were unsuccessful). Such species of *Orcheomyces*, as the author chooses to call the fungi for convenience, are described in detail as to their structure and behavior in the culture. For the first time a study of their enzymes has been made, and the endophytes were grouped accordingly on the basis of their biological relations to the orchids. In general they have thin-walled, regularly septate mycelia; the hyphae are sharply differentiated into *Langhyphen* that branch little and show unlimited growth in one direction, and *Kurzhyphen* that are of smaller caliber and arise at regular intervals and whose cells under certain conditions are transformed into spores (*Sporenträger*) or absorptive hyphae (*Sanghyphen*). In old age spores and hyphae contain a fatty oil. Chains of hyaline or slightly colored spores may unite into loose clusters or closer sclerotia-like groups. All fungi fuse or anastomose in some manner. The hyphal cells contain two to ten nuclei, but the spores contain only two nuclei. Spiral knots initiated in cultures by the surface tension of a drop of water at the tip of the hypha are comparable to those in the root cells developed in response to the pressure of the resisting plasma membrane to the penetration of the hypha. No sexual reproduction was observed.

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[1] BURGEFF, HANS, Die Wurzelpilze der Orchideen; ihre Kultur und ihr Leben in der Pflanze. 8vo. pp. 207. *pls.* 3. *figs.* 38. Jena: Gustav Fischer. 1909.

———, Zur Biologie der Orchideen Mycorhiza. pp. 66. Inaug. Diss. Jena: Gustav Fischer. 1909.

Of the carbohydrate culture media, starch, maltose, and saccharose were best; glucose and dextrin next; and glycerin poorest. Correspondingly, all fungi possessed diastase and emulsin; some invertase and maltase; some aesculin; one tyrosinase; and only one cytase. In humus decoctions all grew well.

The endophytes cannot assimilate free nitrogen. They belong to BENNECKE's category of "Ammon-nitrit-nitratpilze," and grow luxuriantly, forming spores on ammonium salts, ammonium nitrate holding first place. Organic N compounds were varyingly well assimilated. Peptone produced splendid growth, and salep furnished sufficient N for all to grow. All fungi possess proteolytic enzymes.

The production of acid in assimilation is slight, and in general, in media containing asparagin, peptone, or urea, is in proportion to the intensity of the growth. Orchid fungi require to a high degree atmospheric oxygen, dying in long-continued anaerobic cultures. The formation of spores and spore sclerotia depends upon the concentration of the medium, its exhaustion, and the amount of assimilation products present. Salep always stimulated spore-formation, as did increased transpiration.

2. *The study of the plant and the fungus.*—For the biological relations of the plant and the fungus, BURGEFF chooses the terrestrial orchid *Epidendrum* (*dichromum?*) and the hybrid epiphyte *Laelio-Cattleya*. Without a fungus, seeds of *Epidendrum*, on a culture medium of rain water, 2 per cent salep, and 1.5 per cent agar, did not germinate. With ten different fungi they germinated within 25 days. The embryo did not become green until infected. Thinned nutritive agar cultures with fungi produced stouter plants than the rain water cultures. The stages of development and limits of the fungus agree with the *Cypripedium* type of development described by BERNARD. Infection takes place through the suspensor at first, and later through the root hairs, passing by means of the *Durchlasszellen* into the cortex. The hyphae of the sub-epidermal layer (*Pilzwirtzellschicht*) are never digested, but *Eiweisshyphen* appear in the digestive layer beneath. The cytological facts agree with the phenomena of digestion, where the remains (a clump) are surrounded by a cellulose layer (*Haut*), and the nucleus assumes the resting stage, ready to digest new hyphae. Clumps may become several-layered.

BURGEFF found that the seeds of *Laelio-Cattleya*, wettable only after three or four days, could germinate, become green, and attain considerable differentiation (stomata at apex, rhizoids at base, leaf primordia) in three or four months. A resting period of a year is necessary before growth continues, for which also a fungus is required. Just before infection, the oil in reserve in the cells near the suspensor is transformed to starch, which disappears, however, as soon as the fungus penetrates the cells. Both embryo and fungus show evidence of growth, the latter by the formation of *Eiweisshyphen* (homologous with spores and hyphal knots).

Testing the possibility of saprophytic germination in *Laelio-Cattleya*,

BURGEFF obtained its development, in 0.33 per cent cane sugar with mineral salts on agar, in the dark, to the differentiation of papillae, and it lived ten months. Further development either in light or dark required the fungus. While in the light the orchid developed normally, in the dark it elongated and resembled the *Epidendrum* which grew in the weaker concentration of salts. BURGEFF concludes that physiologically the behavior of the fungus is alike in the germination of the epiphyte and the terrestrial orchid, and that the appearance of chlorophyll in the epiphyte is an adaptation to its life in the light.

Seedlings with the fungus in absence of CO_2 in the dark grew, but developed no root, while in the light the growth was normal. Experiments on the physiology of nutrition, where fungus and seedling were grown together, showed the best N sources to be ammonium chlorid and nitrate. Although asparagin was favorable for the fungus in free culture, the plant could not grow in it. In N-free media there was no development. Lactic acid (2 per cent) in mineral salt agar culture caused both plant and fungus to grow well. *Laelio-Cattleya* was found to harbor some fungi (17 tested) unable to stimulate its germination.

BURGEFF devotes 50 pages to the histological processes in the growing plants. These detail the places of entrance, position of the fungi, peculiar features in the plant cell (spores and clumps, *Klumpenbildung*), the emission of hyphae to the substratum, etc. Most of the fungi have mycelial connections with the outside substratum, therefore anatomically there is nothing to prevent ascribing to such hyphae the function of conduction of soluble materials. The author explains the unwettability of the seeds as due to the *Luftbläschen* in the netted testa itself, and to the air between the testa and embryo (comparable to the condition in the lycopod spores). Such unwettability hinders the passage of spores through the soil, contrary to the theory of KOCH and LÜSTNER, but is of advantage in preventing the clinging together of seeds in the capsule, therefore an adaptation to their dissemination by wind. Also because the seeds are chemically attracted to the fungi, the unwettability is an adaptation in terrestrial orchids against too rapid exhaustion of this substance.

BURGEFF agrees with BERNARD in the probable steps of development of the symbiosis by way of parasitism, but would speak of the association not as a "maladie bienfaisante," but as of "einem glücklichen Zusammentreffen verschiedener Umstände." He bases this remark on the following facts: the fungus is harmless, its enzymatic qualities separating it from comparison with parasites with toxic qualities; it is able to kill an unadapted fungus whose penetration it nevertheless allows; its fitness for infection is seen in the *Durchlasszellen* of the embryo. A mutualistic symbiosis demanded by the definition is found in this association, for the orchid has to thank the fungus for its existence, and the fungus is grateful to the orchid for the materials difficult to obtain from the soil which enable it to form spores. As to the materials of exchange between the components, the question is left unanswered; but the idea of conduction of mineral salts is favored, because of the results of the

cultural experiments and because of the detailed morphological and anatomical features of both symbionts. The fungus causes the conversion of starch into sugar by its diastase. Its function results from its enzymatic quality, which, with the solution of carbohydrates in the plant cell, induces the development of the seed, not by bringing soluble materials to the cell, but by transforming substances already there. BURGEFF suggests here the unproven fact of diffusion of the diastatic enzyme out of the fungal hypha through the *Plasmahaut* into the plant cell. This may also occur in the substratum from the emission hyphae. The osmotic relations arising from the sugar solutions could account for the absorption of water, but if nutritive salts are absorbed from the fungi from outside, a rapid change in permeability and adjustment of pressures at just the proper time to seize the salts brought by the fungus must take place.

On the whole, the relations between the plant and the mineral salts of the soil are of striking importance for the origin and maintenance of the orchid symbiosis. Although the structures show a gain in nitrogenous substances, the habitats of orchids, and cultural experiments exclude the possibility of free N-absorption. No anatomical features can prove the absorption of organic carbohydrates; although diastase and emulsin are common to all fungi, material for the action of the former is lacking in the soil, and we are in ignorance concerning the substance in the soil digested by the latter. Any substance taken up by the plant, either through its roots or by means of the fungus, must first be made soluble by the fungus itself, or by its exoenzymes in the substratum.—GRACE L. CLAPP.

MINOR NOTICES

Farm weeds.—The preparation of a scientific manual for the use of the ordinary layman is admittedly a difficult task, but it has been successfully accomplished by CLARK and FLETCHER,[2] whose volume upon farm weeds is the best that has yet appeared upon this subject. The remarkable simplicity without the sacrifice of scientific accurracy is due largely to the splendid ability of the late Dr. JAMES FLETCHER, who thus adds one of the latest of his many valuable contributions to botany and agriculture. More than 200 of the more troublesome weeds of Canada are arranged according to modern botanical classification, with very complete scientific and common synonyms, and briefly but accurately described in non-technical language. Special attention is directed to the characteristics which make the various plants troublesome as weeds, and careful directions are given for the most practicable and successful methods of control and extermination.

The most valuable aid to the recognition of different species is a series of 76 full-page plates, colored with the greatest accuracy. They include

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[2] CLARK, GEORGE H., and FLETCHER, JAMES, Farm weeds of Canada. Second edition. 8vo. pp. 192. *pls. 76*. Ottawa: Department of Agriculture, Dominion of Canada. 1909. $1.00 (single copies only, for sale by Superintendent of Stationery, Government Printing Bureau, Ottawa).

representatives, in natural size and also much enlarged, of the seeds of 100 of the most troublesome species. These illustrations are from the water-color sketches of NORMAN CRIDDLE, and will enable the farmer to identify readily most of his plant enemies, either while they are growing in the field or while polluting his seed grain.

The book is well printed and strongly bound, which, together with its other admirable qualities, makes it a valuable addition to the literature of economic botany.—GEO. D. FULLER.

A text-book of pharmacognosy.—A fourth edition of KRAEMER'S *Text-book* has appeared.[3] It is "intended for the use of students of pharmacy, as a reference book for pharmacists, and as a handbook for food and drug analysts." Such a statement indicates that the volume does not fall within the province of a botanist for review, and yet the material presented is of great interest to botanists. Part I (pp. 222) is entitled "Botany," and comprises a presentation of all the great groups, "outer morphology of angiosperms," "inner morphology of the higher plants," "classification of angiosperms yielding vegetable drugs," and "cultivation of medicinal plants." Of course this is botany for the pharmacist, and Dr. KRAEMER is in a position to know what the pharmacist needs. Only the first chapter, dealing with the great groups, really pertains to the non-pharmaceutical botanist. Perhaps it makes no difference to the students concerned, but the very antique flavor of the presentation of the great groups is somewhat surprising to the modern morphologist. Part II (pp. 383) is entitled "Pharmacognosy," and deals first with crude drugs, and then with powdered drugs and foods. Part III (pp. 88) is entitled "Reagents and technique"; and part IV (pp. 38) deals with "Micro-analysis."

The volume is certainly a thesaurus of information for the pharmacist, and doubtless will have great influence upon the progress of pharmacognosy in this country. There is abundant evidence, also, of an immense amount of painstaking labor on the part of the author, who is to be commended for his many years of faithful effort to organize and advance his subject.—J. M. C.

A naturalist in the Bahamas.—Under this title a memorial volume in honor of Dr. JOHN I. NORTHROP has appeared.[4] The botanical papers are as follows: "Flora of New Providence and Andros (Bahama Islands)," by ALICE R. NORTHROP (reprinted from Mem. Torr. Bot. Club **12**:no. 1. 1902); "Plant notes from Temiscouata County, Canada," by JOHN I. and ALICE R. NORTHROP (reprinted from Bull. Torr. Bot. Club **17**:1890); "Notes on the plant distribution of Mt. Washington, N.H.," by JOHN I. and ALICE R. NORTHROP; and

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[3] KRAEMER, HENRY, A text-book of botany and pharmacognosy. pp. viii+888. Philadelphia and London: J. B. Lippincott Company. 1910. $5.00.

[4] A naturalist in the Bahamas. JOHN I. NORTHROP. Oct. 12, 1861—June 25, 1891. A memorial volume edited with a biographical introduction by HENRY FAIRFIELD OSBORN. pp. 281. New York: The Columbia University Press. 1910. $2.50.

"A study of the histology of the stem of the wax plant, *Hoya carnosa* (L.) R. Br.," by JOHN I. NORTHROP.—J. M. C.

NOTES FOR STUDENTS

Prothallia of Lycopodium.—BRUCHMANN[5] has completed the life histories of *L. clavatum*, *L. annotinum*, and *L. Selago*, with an account of the growth of the prothallia from the germination of the spores to the maturing of the sex organs, and with the study of the embryo development of *L. Selago*. Previously the germination of only three species was known, all with a prothallium containing chlorophyll and belonging to the *cernuum* type: *L. salakense*, independent in development and free from a fungus; *L. cernuum;* and *L. inundatum*, dependent for complete development upon an endophytic fungus.

The germination of the spores was secured by sowing them in the forest where they were found. This was done in two ways: (1) by putting spores and species of fresh strobili into flower pots in potting soil (peat, leaf mold, manure, sand) and forest soil and sinking them in the ground; and (2) by mixing spores with forest soil and burying them in holes 10 cm. deep. The germination of *L. Selago* occurred in 3–5 years after sowing; that of *L. clavatum* and *L. annotinum* in 6–7 years. Prothallia bearing mature sex organs appeared first in *L. Selago* 6–8 years after sowing; in *L. clavatum* and *L. annotinum* in 12–15 years. Practically all the spores of a sporangium of *L. Selago* germinated, but only about 5 per cent of those of other species. All three species develop independently a five-celled chlorophyllose prothallium, after which a fungus is necessary to complete the development. *L. clavatum* and *L. annotinum* develop in the same way, while *L. Selago* forms a type by itself.

The first division, an irregular one, cuts off a small lens-shaped cell at the base of the spore. Although containing food substances, it is poor in cytoplasm and never enlarges. BRUCHMANN considers it a rudimentary rhizoidal cell, homologous with the first rhizoid of the true ferns. The second division, occurring after the spore coat bursts, extends an oblique wall from base to apex, bent toward the rhizoidal cell. While in the *clavatum* type this wall divides the prothallium into hemispheres, in the *Selago* type it is sharply bent away from the rhizoidal cell, making the resultant cells unequal. The difference in direction determines the type of prothallium. The basal cell next to the rhizoidal cell never divides. Its sister cell cuts off an inner wedge-shaped cell and an outer apical cell. A fourth wall divides the wedge into an outer peripheral and an inner or central cell. In *L. Selago* the wedge-shaped cell is considered the first segment cut off from the apical cell.

From this point BRUCHMANN divides the growth of the prothallia into three periods, depending upon change in direction and manner of growth.

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[5] BRUCHMANN, H., Die Keimung der Sporen und die Entwicklung der Prothallien von *Lycopodium clavatum*, *L. annotinum*, und *L. Selago*. Flora 101:220–267. *figs.* 35. 1910.

L. Selago resembles closely *L. Phlegmaria* in development, while *L. clavatum* and *L. annotinum* are alike. The entrance of the fungus at the peripheral or basal cell stimulates the apical cell to division. It cuts off from its two sides alternately five or seven segments in the *L. clavatum* type, and fewer in *L. Selago*. This closes the first period.

Extensive growth of both the prothallium and the fungus characterizes the second stage. Rapid radial growth at the apex results in a pear-shaped prothallium. The fungus in the two lycopod types of prothallium represents two species. In *L. clavatum* it forms a peripheral digestive mantle surrounding the central mass of storage cells. Limited from the central cells by a palisade layer, it becomes entirely intercellular. The fungus of *L. Selago* resembles in habit that of *L. Phlegmaria* and fills the entire prothallium posterior to the apical region except the epidermis. The sister cell of a rhizoid, infected by a branch of the mycelium from the hypodermis, serves as an "Expeditionszelle." From it the hypha passes out to the substratum, spraying out into fine branches. To this cell BRUCHMANN attributes the function of chemically attracting the fungus by its enzymes.

The third period has to do with the changes in the apical region. Marginal meristematic cells in *L. clavatum* surround the axial conductive cells, coextensive with the former storage cells. Reproductive organs develop on the margin, antheridia preceding archegonia. Such prothallia may live twenty years. During this period the fungus forms spores. In *L. Selago* the attempt to gain dorsiventrality causes extensive elongation of the prothallium, which at the soil surface develops chlorophyll. The apical growth becomes marginal, the central tissue acting as a storage region. The outer layers on one side develop paraphyses and sex organs; on the other, vegetative cells containing the fungus, which always remains intracellular.

The embryo-development of *L. Selago* agrees in detail with that of *L. Phlegmaria*. The root appears last, later than in *L. clavatum* and *L. annotinum*. The foot is smaller than that of *L. clavatum* and of *L. annotinum*, but less papillate than that of *L. Phlegmaria*. Its continued growth upward bursts the prothallium, whereupon it reaches the light and becomes green.—GRACE L. CLAPP.

Variation in timothy.—An important contribution to the subject of secular variation has been made by CLARK,[6] who has studied the variation in height, weight of forage produced, earliness of bloom, and duration of the period of bloom in timothy (*Phleum pratense*). Data were secured during three successive years on 3505 plants representing 163 pedigrees derived from 22 different states of the United States. As there can be no doubt that timothy, like many other plants which have been studied, consists of a number of distinct hereditary forms or biotypes, the extent of variation, which was found to be

[6] CLARK, C. F., Variation and correlation in timothy. Bull. 279, Cornell University. pp. 301–349. *figs. 111–150.* July 1910.

very great in all characters studied, may not be considered as having great significance, since the bringing in of still other pedigrees from other sections would doubtless have increased the range of variability. No perceptible correlation was found between earliness and height of the plants or between duration of bloom and height of plants. There appeared to be a slight negative correlation between the duration of bloom and weight, but this was very slight and possibly not significant. Between weight and height, as might be expected, there was considerable positive correlation, ranging from 0.274±0.011 to 0.718±0.006. By securing data covering three years from the same series of plants, an interesting new relation has been developed, namely, the correlation between the condition of plants in one year as compared with the same plants in succeeding years, and for this correlation the author gives the name "coefficient of place-variation." This measures the extent to which an individual, found to have a given rank with respect to a variable character in one year, may be expected to hold the same rank in succeeding years, and is a very important consideration from the standpoint of the practical breeder. The correlation coefficients found ranged from 0.382±0.010 to 0.585±0.008. The lowest correlation was found in comparisons between non-consecutive years, as when 1905 was compared with 1907. This would naturally be expected, since there are more disturbing factors in two years than in one. These coefficients are considered rather low, and are taken to indicate the importance of comparing individuals during several years as a safe basis for selection in economic breeding, since there are very good chances that an individual observed to be superior in one season may be inferior in succeeding seasons.—GEO. H. SHULL.

Seeds of horseradish.—It is a well known fact that the horseradish (*Cochlearia Armoracia*) is generally sterile, though it produces a great abundance of flowers and not infrequently produces capsules. BRZEZIŃSKI[7] has induced the development of seeds by removing a circle of the bark from the upper portion of the root a short distance below the collum. Plants so treated produced a considerable number of good seeds, and in one year (1908) he secured 1500 seeds. Of 50 seeds sown in 1907, 30 produced plants, most of which succumbed to disease, but 9 of which grew to maturity. From the same (1906) crop, 200 seeds planted in 1908 produced only 20 seedlings, thus apparently indicating the rapid loss of vitality of the seeds. Only 6 of these reached maturity. These 15 mature seedling plants of the horseradish were not uniform, but were referable to two types, neither of which agreed with the characters of the parent. The ordinary horseradish is intermediate between these two types, though inclining much more strongly to one of them than to the other. Both types of seedlings proved to be somewhat fertile, producing a considerable number of seeds, even without the operation which induced seed-

[7] BRZEZIŃSKI, J., Les graines du raifort et les résultats de leurs semis. Bull. Acad. Sci. Cracovie, Session of July 5, 1909. pp. 392–408. *pls. 12–15.*

production in the parent. Two hypotheses are offered to account for the appearance of these two types among the seedlings: (1) that they are mutations produced as a result of traumatism in accordance with the views of BLARINGHEM; and (2) that the ordinary horseradish is not a natural species as generally believed by taxonomists, but a hybrid, and that the two types of offspring produced from the seeds are partial or complete returns to its parent types. The author inclines to the latter view, and would interpret the sterility of the horseradish as due, not to the accentuated development of fleshy roots, but to a weakening of the sexual development, not infrequently found in hybrids. The reviewer is inclined also to the latter interpretation, and would point out the important bearing the author's method of securing seeds of the horseradish may have in its application to other sterile hybrids. Many experiments have been terminated by the failure of hybrids to produce seeds. It may be that some of these cases will yield to methods of treatment similar to that employed by BRZEZIŃSKI in securing seeds of horseradish.—GEO. H. SHULL.

The ecology of conifers.—STOPES and Moss have discussed the xerophytism of conifers, and now GROOM[8] considers a number of their ecological features. In the introductory statement three problems are outlined: the cause of their xerophytic foliage and tracheidal wood, the cause of their survival in competition with dicotylous trees, and the cause of the suppression of many forms in past ages. GROOM correctly concludes that not all conifers are xerophytic, in spite of their xerophytic leaf structure, calling attention to VON HÖHNEL'S demonstration of high transpiration in the larch, and to his own experiments which show that coniferous wood, in spite of its tracheidal structure, may conduct water with a rapidity equal to that of a rapidly transpiring dicotylous tree. Attention is called to the fact that the aggregate leaf surface of a coniferous tree may exceed that of a dicotylous tree, because of the immense number of leaves. Indeed, GROOM regards the xerophytic structure of the leaf as a necessity in view of the great amount of exposed surface, and he applies the term "architectural xerophytism" to xerophytism that is dependent upon the organization of the plant rather than upon the direct influence of external factors upon the organs in question. In opposition to STOPES, GROOM regards the tracheidal nature of the wood as a feature of advantage rather than a feature necessitated by heredity, and notes that similar wood tends to occur in various evergreen dicotyls. The extinction of many conifers of past ages is attributed to their imperfect acclimatization, to the fact that they have a great number of insect and fungus enemies, and to their relatively slight power to react advantageously to new conditions. However, their architectural xerophytism makes it possible for them to thrive in nearly all situations, from those that are physically or physiologically dry

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[8] GROOM, PERCY, Remarks on the oecology of Coniferae. Annals of Botany **24**:241–269. 1910.

to those that are sufficiently humid to permit the development of luxuriant mesophytic forests. GROOM'S paper is most suggestive, and adds considerably to our knowledge concerning the difficult problem of coniferous xerophytism.—HENRY C. COWLES.

Nutrition of the embryo in Labiatae.—BILLINGS[9] has investigated the nutritive mechanism associated with the embryo sac of certain Labiatae, a subject that deserves more attention from morphologists. The ordinary sac which is oval or elliptical in longitudinal section, and which encroaches uniformly upon the surrounding tissues, has come to be regarded as the more or less fixed "type" of angiospermous sac. Among the Sympetalae especially, however, a much more complex nutritive mechanism has begun to be uncovered, including special digestive layers and special absorptive regions of the sac, the latter usually taking the expression of tubular haustorial extensions. BILLINGS investigated 15 species of Labiatae, representing 14 of the most representative genera. The results were uniform enough and differed enough from other sympetalous groups investigated to indicate that such structures may be of taxonomic and even of phylogenetic value. For example, the Scrophulariaceae previously described usually have a well developed digestive layer ("tapetum"), in addition to haustorial extensions of various kinds; but the Labiatae lack the special digestive layer. There are three features common to the species studied, and possibly to the whole family, to which the author calls attention: the micropylar haustorium (more or less extensively developed), the much-elongated suspensor, and the antipodal canal or process. *Salvia* is an exception to this statement, for it has a short suspensor and no micropylar haustorium; and the two species investigated "are unique in having two haustorial outgrowths, one coenocytic and one composed of ordinary endosperm tissue" (these haustoria are in addition to the well developed antipodal canal). The author thinks that such variations from the general conditions as are shown by *Salvia* "suggest a taxonomic rearrangement."—J. M. C.

Correlation in oats.—WALDRON[10] has compared the height of culm, length of head, number of grains per head, and average weight of grains in a variety of oats growing at Dickinson, North Dakota. The examination of 1000 plants discovered decided negative correlations (-0.595 ± 0.013, -0.511 ± 0.015, and -0.404 ± 0.017) between the weight of grains and number of grains per head, weight of grains and length of head, and between weight of grains and length of culm. He reaches the conclusion that in selecting the heaviest grains in this variety, the breeder selects plants somewhat below the

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[9] BILLINGS, F. H., The nutrition of the embryo sac and embryo in certain Labiatae. Kansas Univ. Bull. **5**:67–83. *pls. 11–14.* 1909.

[10] WALDRON, L. R., A suggestion regarding heavy and light seed-grain. Amer. Nat. **44**:48–56. 1910.

average height, with shorter heads and fewer grains, thus emphasizing the importance of selecting the superior plants instead of the superior individual grains. As this variety of oats was undoubtedly a mixture of several distinct biotypes, it does not follow that the same mathematical results would be found in other varieties composed of different mixtures. The variety with which WALDRON worked may have contained a short-headed, short-culmed, heavy-grained biotype. In some other mixture the heavy-grained biotype might have longer culms, longer heads, and more numerous grains, and it would then give a positive correlation where WALDRON found a negative correlation, but this does not lessen the importance of the conclusion reached that the individual plant and not the individual grain is the proper unit of selection.—GEO. H. SHULL.

Anatomy of the seedling of Trapa.—A short paper by QUEVA[11] on the curious seedling of *Trapa natans* recalls the case of "caulicle" vs. "radicle," the question of the importance of the root as a primarily essential part of a seed plant. The author confirms the observations of previous investigators concerning the marked inequality of the cotyledons, the negative geotropism of the caulicle (which he prefers to call the hypocotyledonary axis), and the presence of internal phoem in the stem and leaves. His own investigation has resulted in the discovery of this internal phloem in the hypocotyledonary axis and in the petiole of the cotyledon. Although he finds in the very tip of the hypocotyledonary axis a vascular condition which is peculiarly root-like (two xylem points alternating with two small groups of phloem), yet he thinks it is not root, because (1) there is no rotation of the strands in successive levels from the tip of the organ to the cotyledonary node; (2) the xylem points are too near the periphery of the cylinder to look like root poles; and (3) the whole organ is covered by epidermis, except at the spot where the suspensor was attached. The growth of the caulicle, or hypocotyledonary axis, is limited; the roots strike out from its side, their vascular strands being inserted on certain metaxylem elements discernible in cross-section on one side of the vascular cylinder.—SISTER HELEN ANGELA.

Sporophylls of Selaginella.—SYKES and STILES[12] have made a very interesting study of the sporophylls of *Selaginella*, finding an amount of variation and a degree of complexity that have not attracted attention heretofore. A few of the more representative species are described and the different forms of the sporophyll are pointed out as "special adaptations for the secure protection of the sporangia." In many sporophylls there is a well developed air cavity in the base, and the authors suggest "that they recall the mucilage

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[11] QUEVA, C., Observations anatomiques sur le *Trapa natans* L. Compt. Rend. Assoc. Fran. Av. Sci. 1909. Congrès de Lille, pp. 512–517. *figs. 2*. 1909.

[12] SYKES, M. G., and STILES, W., The cone of the genus *Selaginella*. Annals of Botany **24**:523–536. *pl. 41*. 1910.

cavities of *Lycopodium* and the parichnos of fossil genera." In some cases the sporophylls are provided with more or less conspicuous dorsal outgrowths, which have been noted heretofore only in a casual way, but not definitely described. Four types of sporophyll are described: (1) with well developed dorsal flap extending freely downward and protecting the young sporangium immediately below it (as *S. rupestris*); (2) with no dorsal flap, the sporophyll being flat and the sporangium exposed (as *S. spinosa*); (3) with a well developed dorsal projection which is not free but decurrent (as *S. helvetica*); and (4) a series in which the dorsal outgrowth is gradually reduced and lost, each sporophyll more and more completely infolding the sporangium below (as *S. flabellata* to *S. apus*).—J. M. C.

Morphology of Callitris.—SAXTON,[13] in continuing his studies of gymnosperms, has given an account of *Callitris*, an Australasian genus of about a dozen species. The one chiefly studied was *C. verrucosa*, but the results doubtless apply to the genus as a whole, since the species are very closely allied. The sporophylls are in alternating whorls of three, each microsporophyll bearing three sporangia, and each of the upper megasporophylls bearing about 15 ovules, the six sporophylls of the ovulate strobilus producing about 60 ovules. The cells of the mature female gametophyte are all binucleate or multinucleate. The archegonia occur in a single group of about 20, never at the apex of the gametophyte, but along the inner side of the pollen tube near its apex. If two pollen tubes are present, two such groups are organized. The proembryo completely fills the archegonium, the arrangement of cells being variable. More than one embryo is formed from a proembryo, and the first two walls are longitudinal, the mature embryo being dicotyledonous. The claim is well substantiated that *Callitris* and *Widdringtonia* are two distinct genera, but that they should constitute a separate tribe (Callitrineae) coordinate with Cupressineae is not so clear.—J. M. C.

Structure of Mitrospermum.—Mrs. ARBER[14] has investigated the structure of the platyspermous seed described by WILLIAMSON in 1877 as *Cardiocarpon compressum*, and occurring in the British Lower Coal-measures. The outer fleshy (forming the wing-like extension), stony, and inner fleshy layers are recognized and described. Two opposite vascular strands arise from the expanded bundle beneath the nucellus and traverse the outer fleshy layer in the principal plane of the seed, probably continuing almost the whole length of the seed. The nucellus seems to have been entirely free from the integument, and in one seed a tissue within the embryo sac was observed, consisting of "irregular roundish cells," which of course represent the female gametophyte. The

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[13] SAXTON, W. T., Contributions to the life history of *Callitris*. Annals of Botany **24**:557–569. *pls. 45, 46*. 1910.

[14] ARBER, AGNES, On the structure of the paleozoic seed *Mitrospermum compressum* (Will.). Annals of Botany **24**:491–509. *pls. 37–39. figs. 2*. 1910.

conclusion is reached that the seed deserves to be removed from *Cardiocarpon*, chiefly on account of its vascular structure, and therefore a new genus *Mitrospermum* is proposed. Whether the seed belongs to *Cordaites* or not was not determined, for the platysperm character can no longer be used as an indication of that group. Sections of unattached seeds must continue to be made, but there is far greater need of sections of attached seeds, for these will probably solve the puzzling embryo situation attributed to paleozoic seeds.—J. M. C.

Phototropism.—NORDHAUSEN[15] offers more evidence against the lens theory of phototropic perception. He finds that leaves of *Begonia* with killed epidermis assume the normal light position, the palisade cells being the perceptive organs. He says that "the epidermis as well as its papillose character are not necessary for light perception." He finds a great difference between the sensitiveness of the two halves of the leaves of *Tropaeolum*, which renders them unsuitable for comparing the effect of light on the wet and dry halves. This plant and method have furnished HABERLANDT with his best evidences for the lens theory. After offering this significant evidence against the theory, he states that HABERLANDT's reply to his former criticism has not rendered that criticism any less applicable. He also holds that the evidence offered in HABERLANDT's later papers is not of a sufficiently critical nature to give the theory any support.—WILLIAM CROCKER.

Carbon dioxid as a fertilizer.—A Berlin company has placed a product on the market known as "Germanol," which consists of an earthy mixture containing about 18 per cent calcinated soda. The company attributes the virtue of this mixture to an increased porosity of the soil following an increase in the proportion of carbon dioxid. MITSCHERLICH,[16] however, is of the opinion that if such a mixture has any value it must be attributed to the action of the carbon dioxid in increasing the solubility of various difficultly soluble soil substances. His comprehensive tests show that increasing the carbon dioxid content of the soil does not result in an increase of plant product; that there is always sufficient carbon dioxid in the soil to render mineral food available; that an increase in the carbon dioxid in the soil does increase the solubility of difficultly soluble substances, but that such increase is superfluous so far as any advantage to the plant is concerned.—RAYMOND H. POND.

Rhizophore of Selaginella.—WORSDELL[17] has used an investigation of the rhizophore of *Selaginella* as the basis of a discussion of the ultimate morpho-

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[15] NORDHAUSEN, M., Ueber die Perzeption der Lichtsichtung durch die Blattspreite. Zeitschr. Bot. **2**:465–506. 1910.

[16] MITSCHERLICH, EILHARD ALFRED, Ein Beitrag zur Kohlensäuredüngung. Landwirtsch. Jahrb. **39**:157–166. 1910.

[17] WORSDELL, W. C., The rhizophore of *Selaginella*. New Phytol. **9**:242–253. *figs. 2*. 1910.

logical categories. He believes that there are "three stereotyped, fixed categories of organs, viz., shoot, leaf, and root," and that there can be no others. "There can be no room in that region of the vegetable kingdom above the level of the homogeneous thalloid types for any organ which is neutral, intermediate, or undifferentiated in character." Incidentally the author furnishes proof, which he says is unequivocal, "that the normal rhizophore has the morphological value of a shoot." This conclusion we are ready to accept, in the absence of any better one, but it is late in the day to defend rigid categories, and to decide what can and what cannot be.—J. M. C.

New genus of flagellates.—GARDNER[18] has described a new genus of flagellates (*Leuvenia*) whose unusual combination of morphological features prevents "any attempt at present to classify it, even to naming the family to which it belongs or in which it has its nearest affinities." The motile, growth, and palmella stages are known. In the growth and mature stages the nuclei and chromatophores are inconstant in number, and in the motile stages contractile vacuoles occur in both anterior and posterior ends, and "pyrenoids, gullet, and stigma are absent." The chromatophores divide by constriction, remain attached for some time by delicate cytoplasmic strands, and are irregular in shape and size.—J. M. C.

Diurnal periodicity in the nitrogen content of leaves.—Investigations hitherto have tended to establish a diurnal periodicity in the nitrogen content of leaves, the fluctuation showing a greater content in the morning than in the evening. CZAPEK, however, in his *Biochemie* states that such investigations should be more comprehensive. With a view to supplying this need, OTTO and KOOPER[19] have made a comprehensive series of analyses which show that even in different stages of development leaves of several different species have a greater nitrogen content in the morning than in the evening. They also found a gradual decrease in the nitrogen content from spring to autumn.—RAYMOND H. POND.

New genera of Chlorophyceae.—GARDNER[20] has described two new genera of green algae growing in association with other marine algae of California. *Endophyton* (*E. ramosum*) is endophytic within the fronds of various species of red algae, and is referred to the Chroolepidae on account of the absence of hair cells, but it has close resemblances to the Chaetophoreae. *Pseudodictyon*

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[18] GARDNER, N. L., *Leuvenia*, a new genus of flagellates. Univ. Calif. Publ. Bot. **4**:97–106. *pl. 14.* 1910.

[19] OTTO, DR. R., and KOOPER, W. D., Beiträge zur Abnahme bezw. Rückwanderung der Stickstoffverbindungen aus den Blättern während der Nacht, sowie zur herbstlichen Rückwanderung von Stickstoffverbindungen aus den Blättern. Landwirtsch. Jahrb. **39**:167–172. 1910.

[20] GARDNER, N. L., New Chlorophyceae from California. Univ. Calif. Publ. Bot. **3**:371–375. *pl. 14.* 1909.

(*P. geniculatum*) occurs among the cells of the cortical layer of species of *Laminaria*, and is also referred to the Chroolepidae. In the same paper a new *Ulvella* (*U. prostrata*) is described, which is epiphytic on *Iridaea laminarioides*.—J. M. C.

Insect galls of Michigan.—Cook[21] has published a list of 59 species of insect galls from Michigan, 31 of them being new to the state. It includes representatives from all the orders of insects that contain gall-makers except the Coleoptera. As there are about 1200 known insect galls in North America, this list of 59 is only a beginning for the state of Michigan.—J. M. C.

Suspensor in Helminthostachys.—Lang[22] has discovered that *Helminthostachys* possesses a massive suspensor closely resembling that of *Botrychium obliquum* described by Lyon. Since Campbell has recorded the same structure in *Danaea*, it is becoming evident that a suspensor among pteridophytes is not a peculiarity of the Lycopodiales.—J. M. C.

Two embryo sacs in Fritillaria.—Lechmere[23] has added *Fritillaria* to the short list of monocotyledons that occasionally develop two megaspore mother cells in an ovule. In this case (*F. messanensis*) the two enlarged mother cells are figured as lying side by side, in immediate contact, both nuclei being in the synapsis stage.—J. M. C.

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[21] Cook, Mel T., The insect galls of Michigan. Mich. Geol. and Biol. Survey, Publ. 1, Biol. Ser. 1. pp. 23–33. 1910.

[22] Lang, William H., On a suspensor in *Helminthostachya zeylanica*. Annals of Botany **24**:611. 1910.

[23] Lechmere, A. Eckley, Two embryo sac mother cells in the ovule of *Fritillaria*. New Phytol. **9**:257–259. *fig. 1*. 1910.

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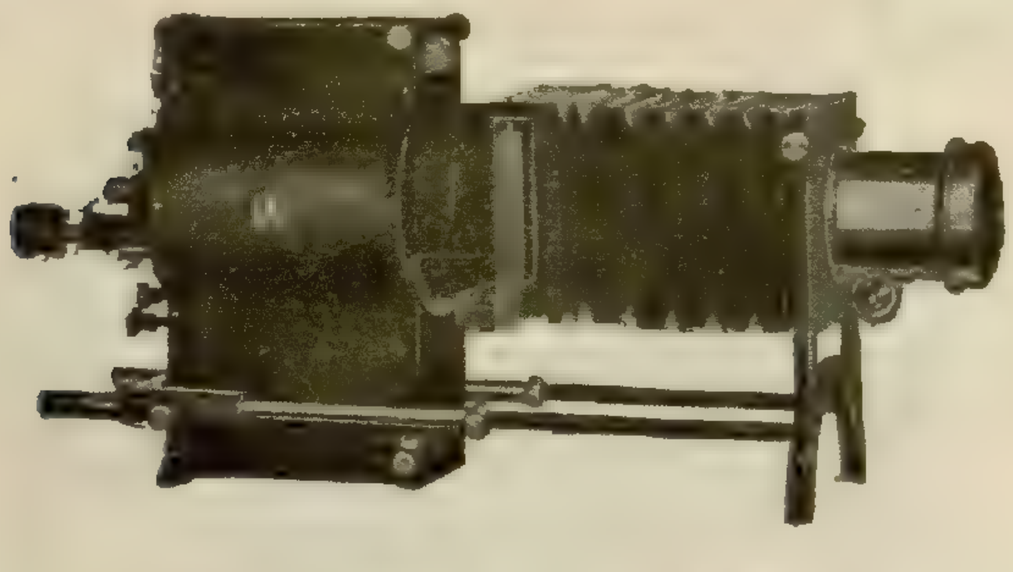

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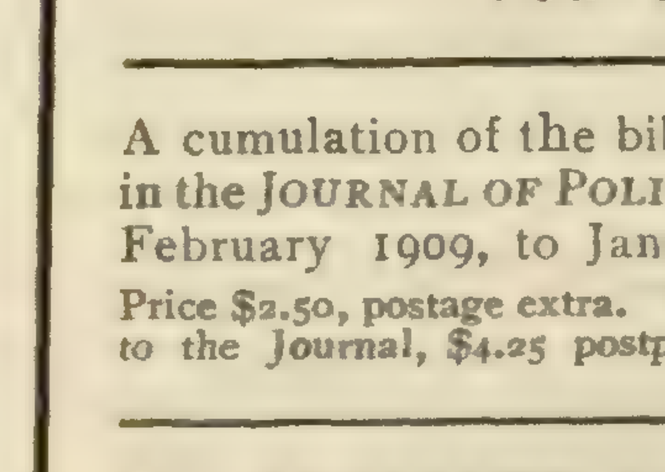

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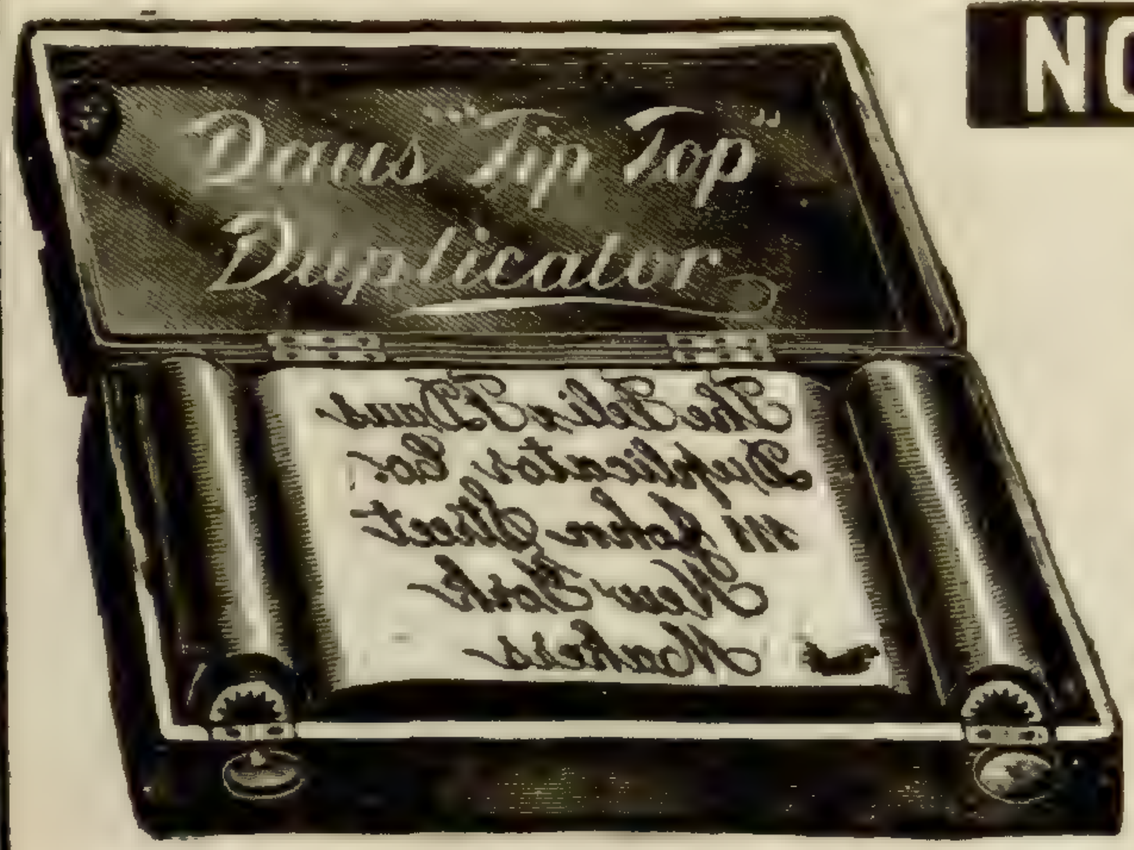

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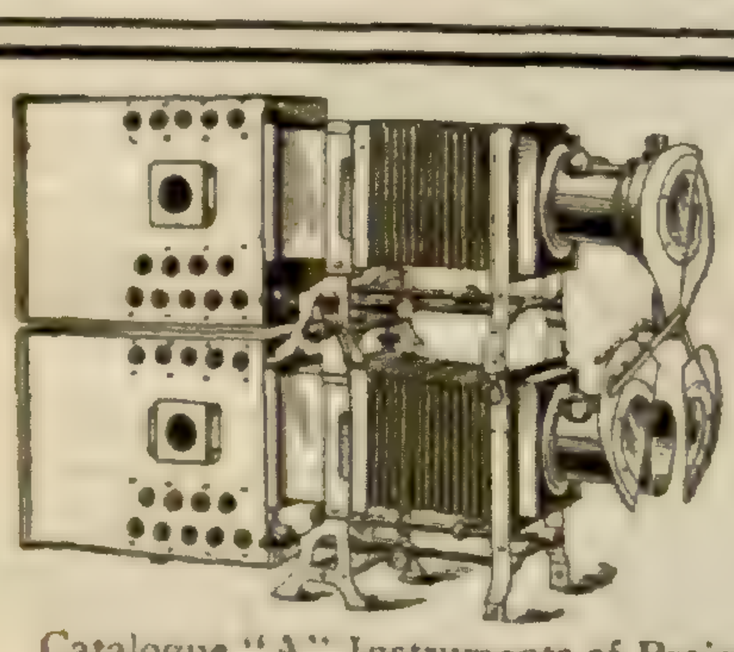

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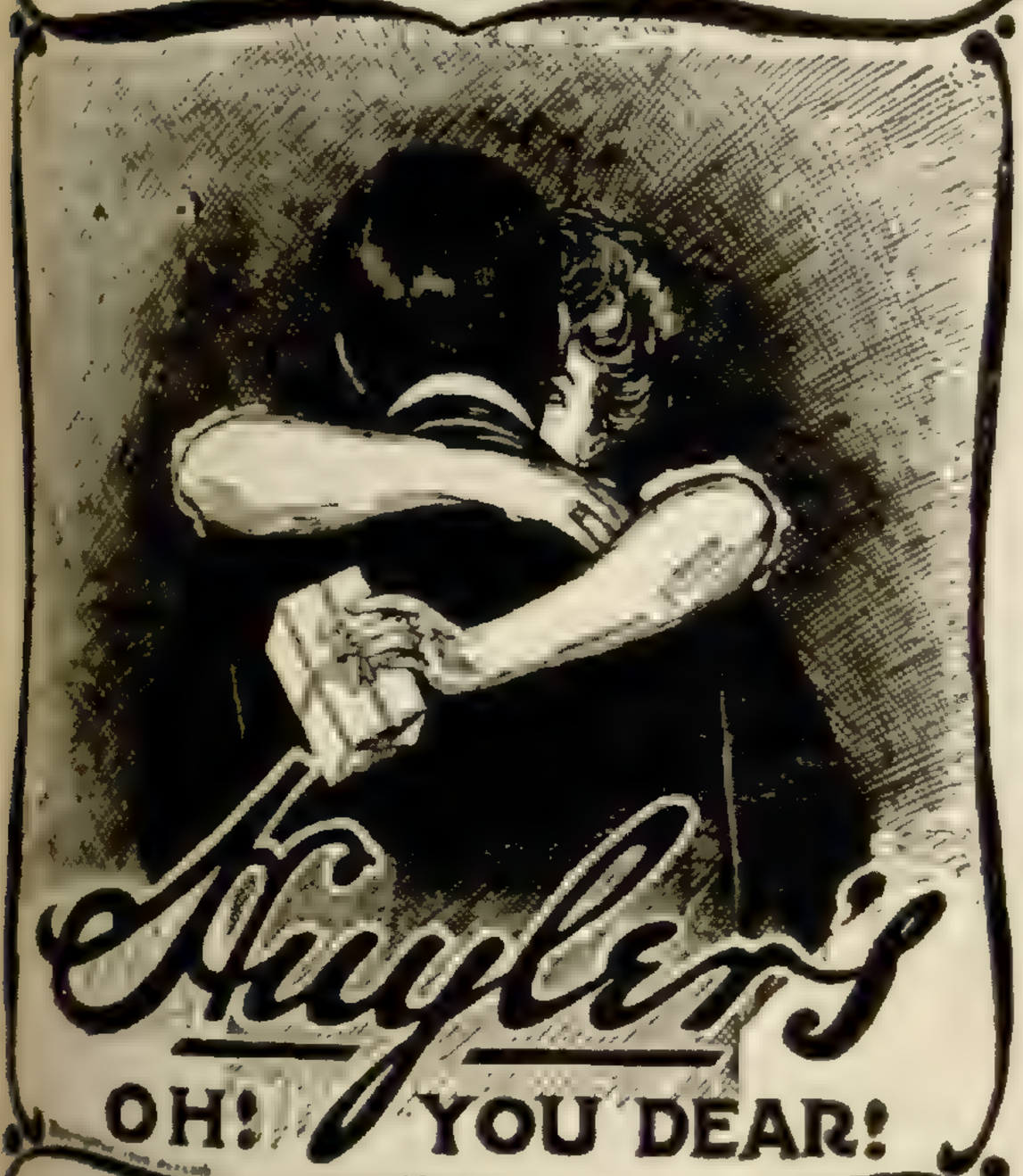

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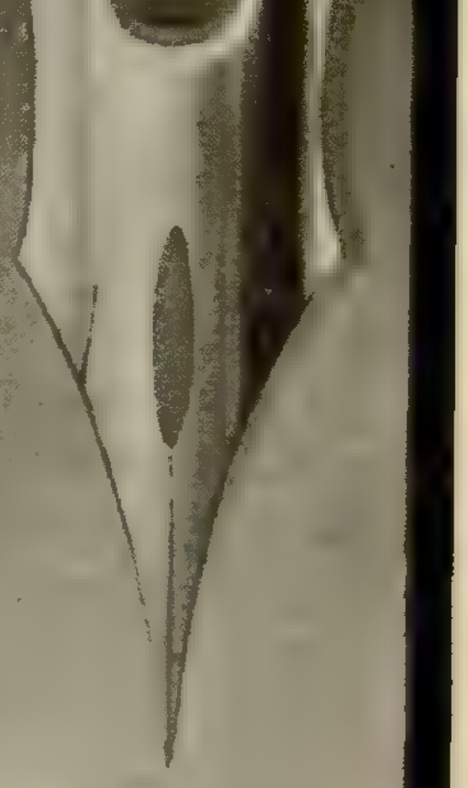

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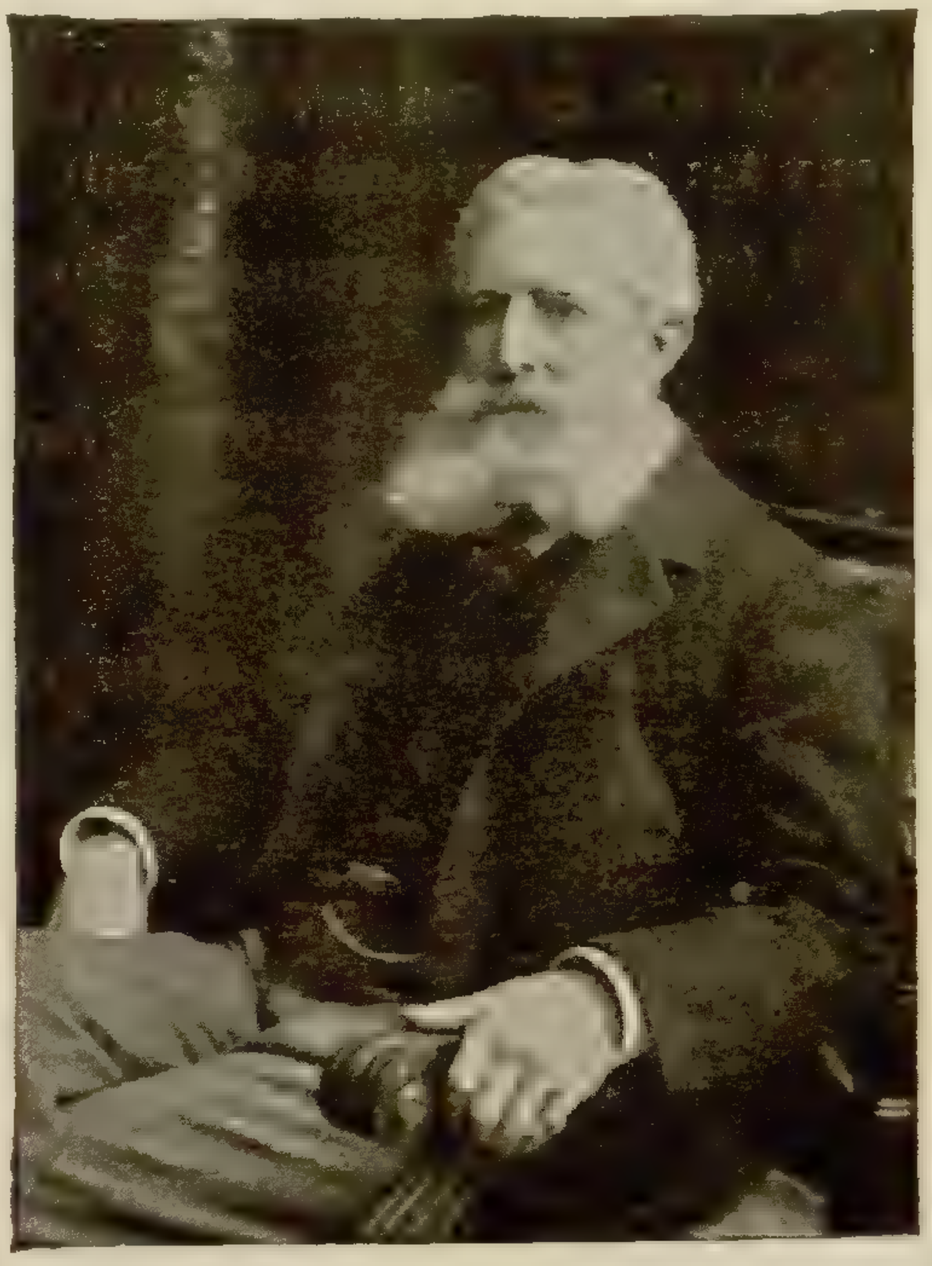

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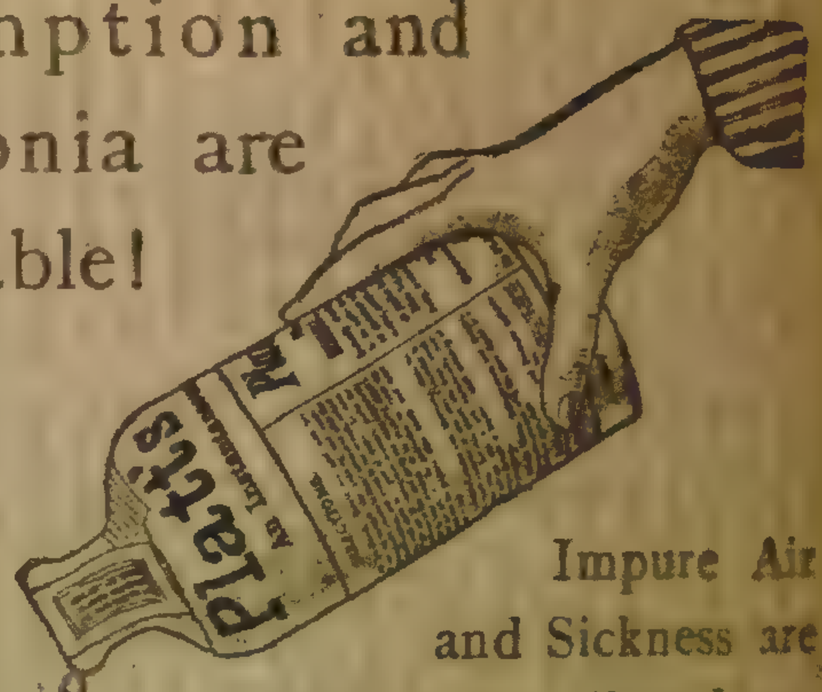

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BOTANICAL GAZETTE

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THE PTEROPSIDA[1]

EDWARD C. JEFFREY

(WITH PLATE XIII)

Two years ago, I published a reply to the various criticisms which had been made from time to time of the great group of vascular plants defined as Lycopsida. At that time a promise was made that the attacks, neither few nor unimportant, leveled at the pendent and corresponding phylum Pteropsida, would likewise be met. In the interval my time has been very much taken up with investigations on the higher seed plants, and it has heretofore been impossible to carry out the intention then expressed. The delay, however, is rather an advantage than otherwise, for it has enabled the opposition to the conceptions connected with the Pteropsida to crystallize and clarify, which materially simplifies the task of criticism. Moreover, in the past two years we have seen venerable but no longer useful morphological doctrines go by the board. Their disappearance is of importance in the present connection, because they have been haled into court in the present discussion.

The validity of the Pteropsida, as a natural phylum, may apparently now be taken as settled, since the group as defined by the present writer has been adopted by a number of botanists, whose knowledge, at once profound and extensive, of living and extinct vascular plants makes their opinion of the greatest weight. There appears accordingly to be no serious opposition at the present time to the conception that all those Vasculares which are

[1] Contributions from the Phanerogamic Laboratories of Harvard University, no. 30.

characterized by palingenetically large leaves and dorsal or abaxial sporangia are in reality so united by a common plexus of origin that they may be with advantage mustered under a common appelation.

Although the standing of the Pteropsida as a large natural phylum of plants now appears to be on a firm footing, the important question of the morphology of the central cylinder or stele of vascular plants is still the subject of much controversy, and the English school of morphologists, led by Dr. D. H. SCOTT, who is himself a host, has attacked the present writer's position with great vigor. The Pteropsida certainly are the appropriate battle ground for the decision of the fundamental morphological question of the internal morphology of the stem, since, unlike the Lycopsida, they are still in full vigor, while they share with the latter phylum the advantage of a very extended history. The most important line of attack is in connection with the morphological status of the pith, which the present writer regards as external tissue included by the stele in the course of evolution. The English anatomists, on the contrary, regard the pith as in all cases a specially differentiated central portion of the fibrovascular tissue itself. Of late, however, the extremity of the English view appears to be modified somewhat by the admission that in certain instances the pith may be derived from outside the stele. Another less important and not generally adopted criticism of the author's views is to the effect that the megaphyllous or large-leaved habit is not a primitive one for the Pteropsida. This criticism has been put forward by only a few of the English anatomists, and appears to have been effectually answered by two recent American writers on the subject.

The lapse of time has made the task of replying to criticisms against the extrastelar origin of the pith a much easier one. The growing-point hypothesis, which has been applied by STRASBURGER to the elucidation of the morphology of the pith, has been recently rejected by a number of morphologists in Europe and America.[2] The interpretation of the mature structure of the organs

[2] JEFFREY, E. C., Morphology and phylogeny. Science N.S. **23**:291. 1906. BOWER, F. O., The origin of a land flora, chaps. xiv and xv. London. 1908. COULTER, J. M., Vascular anatomy and the reproductive structures. Amer. Nat. **43**:219–230. 1909.

of the higher plants in reference to the so-called apical meristems has long dominated morphology of a certain type, although its validity in relation to the histological structure of stems, roots, etc., has never been admitted by such distinguished anatomists as DEBARY and VAN TIEGHEM. It has not been any gain to anatomy that STRASBURGER, a morphologist of the reproductive structures and the cell, should have forced the growing-point hypothesis into the anatomical field in his one important contribution to vegetative histology.[3] It is more unfortunate that his views have been adopted and elaborated by those who cultivate anatomy in England. With the overthrow of the hypothesis in regard to the morphological value of apical meristems, the views of the English anatomists, who have built on this uncertain foundation, have lost a fundamental support. That the application of the hypothesis of apical meristems to anatomical facts leads to hopeless contradictions and logical absurdities the present writer has shown in his article cited above. It appears to be unnecessary to repeat these arguments here.

It must be admitted that the English view, propounded by Dr. SCOTT in a review of the present author's investigations on the stele (*New Phytol.* 1902) and repeated with conviction by nearly all subsequent English writers on anatomical themes, has an air of probability in its favor, in spite of the fact that it can no longer summon to its support the hypothesis of the apical meristems. It seems prima facie improbable that the fibrovascular structures of the stem should be able to surround or contain tissues which primitively lie outside. Moreover, the holders of the view in regard to the stelar origin of the pith have the advantage that their opponents in a measure face the logical impossibility of proving a negative. Although it is not possible to prove in all cases that the pith may be derived from outside the stele, it is fortunately only necessary to demonstrate this in a few instances, in order to invalidate the position of those who claim that the pith is differentiated from the substance of the stele itself.

Professor GWYNNE-VAUGHAN among English anatomists is the one who has shown the greatest openness of mind in regard to the

[3] STRASBURGER, ED., Bau u. Verrichtungen d. Leitungsbahnen. Hist. Beitr. 3:1891.

origin of stelar structures, for, unlike most of his countrymen, he has always been willing to admit that there is some evidence as to the extrastelar origin of the pith in certain instances. To him belongs the credit of having called attention to the fact that in certain of the ferns, structures which are unquestionably extrastelar in their origin may penetrate the central cylinder of the stem.[4] Fig. 1 of the plate accompanying this article shows a transverse section of the stem of *Onoclea* (*Struthiopteris*) *germanica*. The stem is very irregular in outline on account of the crowded leaf bases attached to its surface. The leaf bases, actual or potential, are distinguishable by the fact that they have a double fibro-vascular bundle. In the substance of the stem lie a number of cavities, situated for the most part within the boundaries of the central cylinder, as determined by a line drawn external to its bundles. These cavities are more or less occupied with a filmy substance representing the ramental covering of the epidermis. By inspection of the figure it can be clearly made out that the cavities plugged with *ramentum*, occurring in the substance of the pith, are derived from outside, and represent ingrowths of the external epidermis, including the outside air. Fig. 2 represents a part of a similar section somewhat more highly magnified. On the left may be seen the communication of the medullary pocket with the exterior surface of the stem. It is an axiom with the greater number of the English anatomists, that if pockets or apparent ingrowths of tissues, normally extrastelar, occur within the central cylinder, these are not what they appear to be, namely, incursions of extrastelar tissues into the substance of the stele, but, on the contrary, are merely portions of the stele which have been so transformed as to resemble tissues of the cortex. In the case supplied by our two figures we have a logical *reductio ad absurdum* of the usual English view, for here we have not only the external hairy covering of the stem but even the outside air making their way into the innermost sanctity of the stele. Even the most convinced adherent of the stelar origin of the pith must admit that in this case structures which are quite outside the stele

[4] GWYNNE-VAUGHAN, D. T., On the possible existence of a fern stem having the form of a lattice-work tube. New Phytol. 4:no. 9. 1905.

are able to make their way into it. If it is once conceded that such clearly extrastelar substances as ramentum-covered epidermis and the free external atmosphere are able to make their way into the interior of the stele, there appears to be little ground for questioning that the cortex and its internal boundary, the endodermis, may penetrate the same *sanctum sanctorum*. In the present defunct condition of the growing-point hypothesis, it seems clear, in view of existence of such facts as those illustrated in the two figures just described, that the dogma of the stelar origin of the pith rests on an extremely weak foundation.

It is admitted further, even by those who are most extreme in their support of the view that the pith is always of stelar origin, that, although the central cylinder of the stem cannot include within itself the outlying tissues of the cortex, this possibility exists in the case of the leaf trace. Mr. BOODLE, the most logical and consistent of the younger English anatomists, and one whose contributions, together with those of Dr. D. T. GWYNNE-VAUGHAN, comprise the most important data on the anatomy of ferns which have recently appeared in England, not long since published an article on certain species of *Gleichenia*.[5] He here states that "the nearly circular or subcordiform petiolar bundle of *Eugleichenia* may be held to be derived from the horseshoe-shaped bundle of the *Mertensia* type by contraction, and by the fusion of the free ends of the horseshoe, *the sclerenchymatous cortex in the concavity of the latter thus becoming inclosed*, or at a higher level suppressed"! The present writer has italicized the significant part of the quotation. It is apparent that Mr. BOODLE admits that the foliar trace may include cortical tissue. If such an admission is made in the case of the Gleicheniaceae, it cannot fail of application to the petiolar structures of other families of ferns. Let us take as an example, among many others, the case of the Marattiaceae. In fig. 3 is represented the vascular system of the base of one of the large pinnules of *Angiopteris evecta*. The bundles are arranged in a horseshoe-shaped manner, with the two large bundles terminating the arms of the horseshoe turned inward and downward.

[5] BOODLE, L. A., and HILEY, W. E., On the vascular structure of some species of *Gleichenia*. Annals of Botany **23**:419–432. *pl. 29*. 1909.

Within this horseshoe-shaped cordon of bundles is inclosed a mass of cortical tissue, which to all intents is a pith. Fig. 4 represents a cross-section of the bundle system of the pinnular petiole at a higher level, where, as in *Gleichenia* cited above, the edges of the horseshoe have fused together. It is clear that as a result of this fusion we have a mass of included cortical tissue entirely surrounded by bundles, in other words a condition which the present writer has hypothetically considered to exist in the case of the central cylinder of the stem, where it contains a pith. On the right of the fused horseshoe-shaped complex of bundles two small strands are seen passing off to supply a pinnule of the second order, leaving a gap precisely like that found in connection with the departing leaf traces of the stem or main axis. It is impossible to disregard this obvious resemblance of all the structures in the petiole under discussion to those found in the stem. It is at once suggested that the interpretation of the two sets of facts must be the same, and that if, as is admitted, the petiolar strands are able to inclose tissues of the cortex, there is no reason to question that the same process of the inclusion of fundamental tissues by the fibrovascular system may take place in the stem. This view of the matter gathers force from the hypothesis, which has won favor in England and on the continent, that the leaf of ferns represents only a modified branch. If this view of the morphology of filicinean leaves is adopted, it makes the study of that organ of great use in throwing light on the conditions found in the stem, especially as the leaf by its well-recognized conservatism will supply us with evolutionary stages which have become obsolete in the stem proper.

Fig. 5 represents a cross-section of the entire rachis of *Marattia alata* at a point where the petiolar bundles have formed a closed system by the fusion of the originally free ends of the horseshoe-shaped complex. Here we see precisely the same conditions as are found in the case of *Angiopteris evecta*. Fig. 6 shows the same leaf axis at a higher point, where a vascular supply for a secondary axis is being given off. This plane of section is of special interest because the large medullary bundle formed from the fusion of the two margins of the original horseshoe-shaped complex is func-

tioning in the same way as is commonly found to be the case with the medullary strands of the stem, namely as a reparatory strand to help fill up the leaf gap above the point of departure of the traces. It is clear from what has been stated in the case of *Marattia alata*, just described, that the leaf may develop a vascular system resembling in a detailed manner that found in the case of siphonostelic stems. It seems eminently a sound conclusion to infer as a consequence, since the fundamental tissue of the cortex may readily be included in the fibrovascular system of the leaf trace, that a similar condition may also occur in the stem.

Only two examples have been chosen for illustration of the occurrence of siphonostelic leaf traces, but the genus *Danaea* among the Marattiaceae presents parallel conditions to *Angiopteris* and *Marattia*. Among the other families of ferns the phenomenon is frequently represented. A notable and common case is that of *Pteris aquilina*. Here the sides of the original channel-shaped leaf strand become strongly pushed in, and the fusion takes place so that the joining bundles constituting the margins of the fibrovascular complex of the leaf lie above and outside the siphonostelic lower part of the leaf system. The branches given off to the main ramifications of the leaf are derived from the lateral margins of the siphonostelic region, but in passing off receive a subtending strand from the large upper fused bundle, which lies on the outside of the stelar tube of the leaf axis. The siphonostelic condition in the foliar supply is not confined to the ferns, but is likewise of very frequent occurrence in the angiosperms, where it is susceptible of a similar morphological interpretation. In the case of certain dicotyledons, moreover, diverticula of the epidermis, lined with a hairy covering, make their way into the cavity of the pith of the leaf stalk, showing that here too there is no question of the possibility of extravascular tissues being included within the complex of bundles. It may be further stated that there appears to be no clear distinction between the condition where the cortical fundamental tissues become deeply embayed in the fibrovascular system of the leaf, and where an actual siphonostelic condition results from the fusion of the marginal bundles of the foliar complex. Accordingly it appears strictly logical to include

the deeply infolded petiolar supply of the cycads in our argument. Since the leaf traces of this group originate on the opposite side of the stem from that on which they pass out into their corresponding leaf, it would be necessary to assume that each half of the leaf supply carried with it its own peculiar portion of the medullary parenchyma, and that the fractions were accurately joined with one another in the leaf base, to the exclusion of the fundamental tissue of the cortex, if we were to accept the idea that the fibrovascular tissues are in general unable to embay or include portions of the fundamental tissues of the cortex. This seems much too improbable a supposition to be seriously entertained.

It appears evident, since the stelar system of the stem in the case of certain of the lower Pteropsida, for example, species of *Onoclea*, *Cystopteris*, *Aneimia*, etc., is able to include tissues and substances which are beyond question extrastelar in their origin, that no difficulty arises in regarding the pith present within the siphonostelic central cylinder of the lower (as well as the higher) Pteropsida as morphologically equivalent with the fundamental tissue of the cortex, with which it is often continuous through the gaps in the stelar walls resulting from the exit of the vascular supply of leaves and branches. A further argument in favor of this view is the frequent textural similarity between pith and cortex, even where the former as the result of upward evolutionary changes is no longer continuous with the fundamental tissue without the stele. It follows equally that the morphological doctrine for which STRASBURGER is responsible, and which has been carried to its logical conclusion and *reductio ad absurdum* by the English anatomists, namely, that the criteria of the morphological status of plant tissues are to be derived from a study of the growing point of the mature organ rather than from comparative anatomical considerations and particularly from a study of the seedling, falls to the ground.

It is now possible to consider with advantage the alleged primitive absence of foliar gaps in the Pteropsida, which has recently been asserted by GWYNNE-VAUGHAN in connection with studies on fossil representatives of the Osmundaceae. In the genus *Thamnopteris*, this author has found the center of the stele to be

occupied by a large mass of short tracheids, which he has interpreted as a pith of stelar origin. To state that a central mass of tissue, which according to the author's own admission is entirely tracheary, is the forerunner of the pith, and proves the origin of the latter from tissues of the stele, is apparently a clear case of begging the question. The example of another fossil osmundaceous genus, *Zalesskia*, which has also been brought into court by GWYNNE-VAUGHAN, is equally inconclusive, since the central tissues in the two species of this genus described are in a very bad condition of preservation. Naturally enough, in these obviously protostelic representatives of the Osmundaceae, this author found no evidence of the presence of foliar gaps. A much stronger argument in favor of his view is furnished by the fossil genus *Osmundites Dunlopi*. Here in sections of the very badly preserved stem it was impossible to distinguish clearly any foliar gaps. GWYNNE-VAUGHAN assumes that the obviously much contracted central cylinder of his *Osmundites Dunlopi* represents the primitive conditions in the Osmundaceae, and shows that foliar gaps were originally absent in this family. It is not less reasonable to suppose that the nearly contemporary *Osmundites skidgatensis* from the Lower Cretaceous of the western coast of the Dominion of Canada, in which the foliar gaps are very large and in which the pith very clearly communicates with the histologically strikingly similar tissues of the cortex, in reality represents the primitive condition for the Osmundaceae. All that the fossil evidence enables us to state regarding the Osmundaceae, which constitutes the only evidence for GWYNNE-VAUGHAN'S hypothesis of the original absence of foliar gaps in the fern series, is that the Osmundaceae varied more in structure in both directions during the Mesozoic than they do at the present time, in other words they presented a more generalized condition.

The evidence from the comparative anatomical and developmental standpoints is, on the contrary, clearly all in one direction. Mr. SINNOTT in a recent article[6] has shown that in the genus *Todea*, especially in the filmy subgenus *Leptopteris*, there is fre-

[6] SINNOTT, E. W., Foliar gaps in the Osmundaceae. Annals of Botany **24**: 107–118. *pls. 11, 12.* 1910.

quently an apparent absence of foliar gaps, but that in all the species which he studied in serial sections a gap was really present, although in a single section it might appear to be absent. Moreover, it was shown by this author that in the case of the horseshoe-shaped stele of the leaf in species of *Osmunda* and *Todea*, the passing off of the pinnular traces always left clear gaps in its wall. Moreover, both Mr. SINNOTT and Professor FAULL[7] have made it quite clear that the hypothesis of GWYNNE-VAUGHAN as to the primitive absence of foliar gaps in the Osmundaceae receives no support whatever from a consideration of the anatomy of the seedling of living species. Consequently, we may say of the hypothesis advocated by GWYNNE-VAUGHAN that it is not definitely confirmed by the fossil evidence, and that all the evidence derived from the consideration of the anatomy of the stem, leaf, and seedling of living species is entirely against his view. It may consequently be stated with confidence that at the present time there is no valid proof in favor of the original absence of foliar gaps in the Osmundaceae.

The English school of anatomists has been well advised in making its stand upon the stelar origin of the pith as opposed to its derivation by the inclusion of extrastelar fundamental tissue within the central cylinder, for if that view is once overthrown, a number of other conceptions commonly held in England fall with it to the ground. If it be clear that the pith is originally an inclusion of the fundamental tissues within the central cylinder, certain interesting conclusions immediately follow. One of the most important and far-reaching generalizations of modern plant anatomy, and one which receives the fullest support from the considerations of all the main groups of vascular plants, is that the foliar strand perpetuates the original condition of the wall of the stelar tube. There is distinct evidence in the case of the Osmundaceae, Ophioglossaceae, Lyginodendreae, Equisetales, etc., that the central cylinder of the stem was once composed of concentric fibrovascular bundles, since bundles of this type persist in the leaf trace or sporophyll trace of these various groups. This inevitably follows if it is admitted, as apparently it must be from

[7] FAULL, J. H., The stele of *Osmunda cinnamomea*. Trans. Canad. Inst. 8:515–534. 1909.

the application of sound logic to the known facts, that the pith in these families or orders is morphologically included fundamental tissue.

On the basis of conclusions drawn from the leaf trace in existing pteridophytic groups, we must regard the concentric as the primitive type of fibrovascular bundle. This view of the matter is strengthened by the fact that the concentric bundle is characteristic of the phylogenetically older representatives of the Pteropsida. In the case of the Lycopsida, unfortunately, the evidence is very defective, since this phylum reached its culmination in the remote past and is now almost extinct. The English view of the matter is diametrically opposite, namely, that the collateral bundle is more ancient and that the concentric type has been derived from it. It has been cited in favor of this view, originally by Dr. SCOTT and afterward by nearly all the younger English anatomists, that no evidence is forthcoming in favor of the superior age of the concentric type of bundle in the case of the seedling of the ferns which have collateral stem bundles in the adult. This statement appears to be entirely fallacious. In the first place it would be just as reasonable to assume that centripetal or cryptogamic xylem was not originally present in the stem bundles of our existing gymnosperms, because forsooth it has never been found in the seedling stem. The present writer entirely agrees with the English anatomists in the conviction that centripetal xylem was once well developed in the stem of the ancestors of the living gymnosperms, but this conclusion rests on the persistence of this type of xylem in the leaf trace of forms actually living or their immediate ancestors. On the same basis of argument, concentric bundles were originally present in the stems of those few ferns which today show a collateral condition in their cauline system, for here, as in the gymnosperms, the structure of the leaf affords evidence which is no longer supplied by the seedling. Moreover, if the collateral type of bundle is really primitive for the fern series as a whole, one would expect to find some evidence of its presence in the seedlings of the extremely numerous modern ferns which are characterized by the presence of concentric bundles both in their stems and leaves. Although a great deal of attention has been devoted by

the younger English anatomists to hunting for such evidence in fern seedlings, success has not crowned their efforts. Moreover, if the collateral type of bundle really be primitive for the existing ferns, we should expect to find this condition present in the bases of their foliar organs. It follows, from all the considerations mentioned above, that the absence of the concentric condition in the seedlings of the comparatively few existing ferns showing collateral organization in their adult cauline system constitutes no valid argument against the primitiveness of the concentric bundle for the stem of these and of ferns in general. The evidence considered in connection with the extremely sound and satisfactory generalizations concerning the conservative character of the leaf trace, to which the English anatomists have contributed so honorable a share, is entirely in favor of the concentric as the primitive type of cauline bundle in the fern series.

It follows that none of the recent work overthrows the generalizations put forward in the writer's earlier memoirs as to the phylogeny of the stem in the vascular series. It now in fact appears much more clearly than formerly that the primitive condition of the vascular system in both stem and leaf in the Vasculares as a whole was what the present writer has designated protostelic, that is, a condition in which the fibrovascular tissues harbored no pith. Following this condition was one in which the fibrovascular system became transformed, especially in the more progressive stem, into a stelar tube lined both internally and externally with phloem and endodermis. In the process of time the internal phloem became degenerate, probably on account both of the absence of direct relation to the leaves and of the appearance of secondary growth, advantageously localized ultimately on the outer surface of the stele. The internal endodermis more slowly followed the internal phloem into oblivion, and is often found at the present time in the young individual where it is absent in the adult (Ophioglossaceae, Equisetaceae, Ranunculaceae). The pith must in all cases be regarded as a derivative of the cortex, which has become more or less completely sequestered within the stele. The tubular stele may with propriety and accuracy continue to bear the designation siphonostelic, a term moreover which, in addition to having

an apparently wider and truer significance than the English term solenostelic, holds the claim of priority.

NOTE ON THE LYCOPSIDA.—In the second edition of his admirable *Studies in fossil botany*, Dr. SCOTT adopts without question the present writer's phylum Pteropsida. He also adopts the designation Lycopsida, but confines its application to the Lycopodiales, living and extinct. For the remaining groups included in the present writer's Lycopsida, he proposes the name Sphenopsida, since he regards the Equisetales, Psilotales, and Sphenophyllales as not properly microphyllous, or to be included in the same phylum as the Lycopodiales. This view does not appear to be well founded, since the Equisetales and Psilotales are on anatomical grounds clearly and unquestionably microphyllous and likewise ventrisporangiate. There is no anatomical evidence as to the microphyllous character of the Sphenophyllales, since their central cylinder is protostelic. They resemble the two series mentioned, however, in being ventrisporangiate. The writer is of the opinion that the forking and arrangement of the fibrovascular strands in the blade of the leaf affords an unreliable criterion as to affinities, since if we considered the forking leaf trace rather than the relation of the foliar strands to the stele of the stem, it would be necessary to include certain Sigilliarieae with the Lycopsida in the sense of Dr. SCOTT and others with his Sphenopsida. A forking leaf trace and even a large leaf blade may occur in the lycopsid series, but neither of these is a palingenetic feature, as is clearly shown by the relation of the leaf trace to the central cylinder of the stem. There appears, in view of the considerations just described, no reason of sufficient weight for excluding the Equisetales, Psilotales, and Sphenophyllales from the phylum Lycopsida, since they possess all the essential characters of this great group. At best these three series can be aggregated only as a subgroup under the main heading Lycopsida.

NOTE.—It is a fact, apparently not without significance, that the various recent English writers, who are impelled to disagree with the present author's views as to the absence of foliar gaps in the Equisetales, have not made any reply to the seemingly unanswerable arguments in favor of these views, but have contented themselves with the mere reiteration of a dissentient opinion.

The conviction is continually repeated, in recent English publications bearing on this subject, that the gaps above the leaf traces in the modern Equisetales, but separated from their supposedly corresponding traces by the whole thickness of the so-called nodal wood, are in reality foliar gaps. An insuperable difficulty in this view, in addition to the very important anatomical ones cited by the present writer, is the fact that in both paleozoic and mesozoic representatives of the Equisetales the supposed foliar gaps are sometimes twice as numerous as the traces. It follows, of course, that some of the putative foliar gaps were not in reality leaf gaps in the older representatives of the Equisetales. This state of affairs, brought into strong prominence by recent Swedish investigations on mesozoic Equisetales, seems to furnish the necessary *coup de grace* to the views tenaciously held in England.

SUMMARY

1. The Pteropsida represent a great natural phylum of vascular plants characterized by dorsisporangiate sporophylls and by palingenetically large leaves, as inferred from their anatomical relations.

2. The pith of the Vasculares, in all cases where definite evidence is available, is an inclusion of the fundamental tissues of the cortex on the part of the stele.

3. The concentric type of tubular central cylinder is more ancient than the collateral and antedates the latter, as is shown by the persistence of the concentric condition in many leaf traces, where it has become obsolete in the stem.

4. So far as the primary bundle system of the Vasculares is concerned, they present a reduction series, in which the ferns and lower gymnosperms (Archigymnospermae) represent the earlier and more complex stages, and the higher gymnosperms (Metagymnospermae) and dicotyledons the phases which are more recent and more simplified.

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EXPLANATION OF PLATE XIII

FIG. 1.—Transverse section of the stem of *Onoclea Struthiopteris;* ×5.

FIG. 2.—Transverse section of a part of the stem of the same species; ×10.

FIG. 3.—Transverse section of the base of the pinnular axis of *Angiopteris evecta;* ×10.

FIG. 4.—Transverse section of the same at a higher level, showing the fusion of the marginal bundles of the foliar system; ×10.

FIG. 5.—Transverse section of the rachis of *Marattia alata;* ×10.

FIG. 6.—The same, showing the exit of the vascular supply of a secondary axis; ×10.

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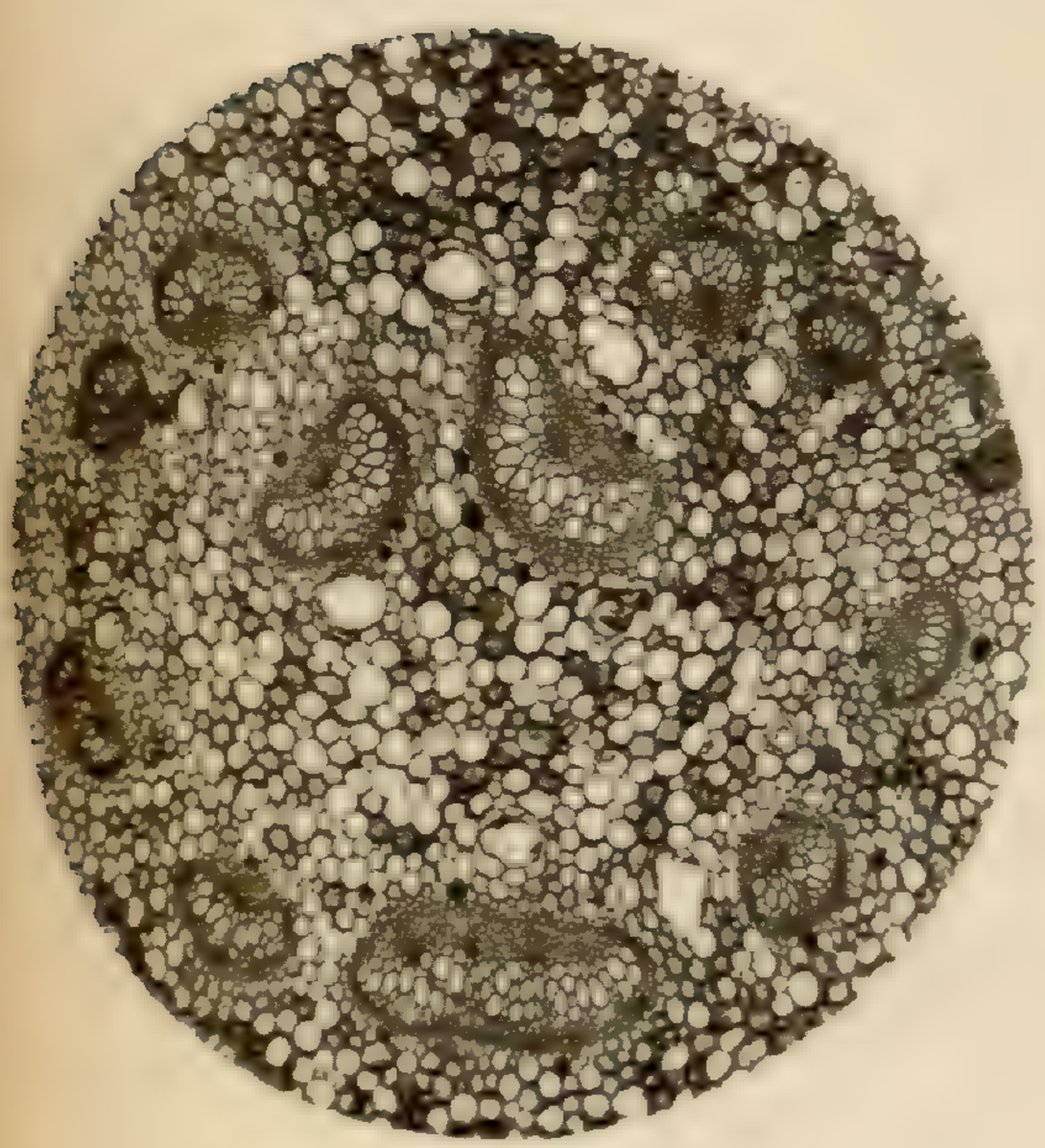

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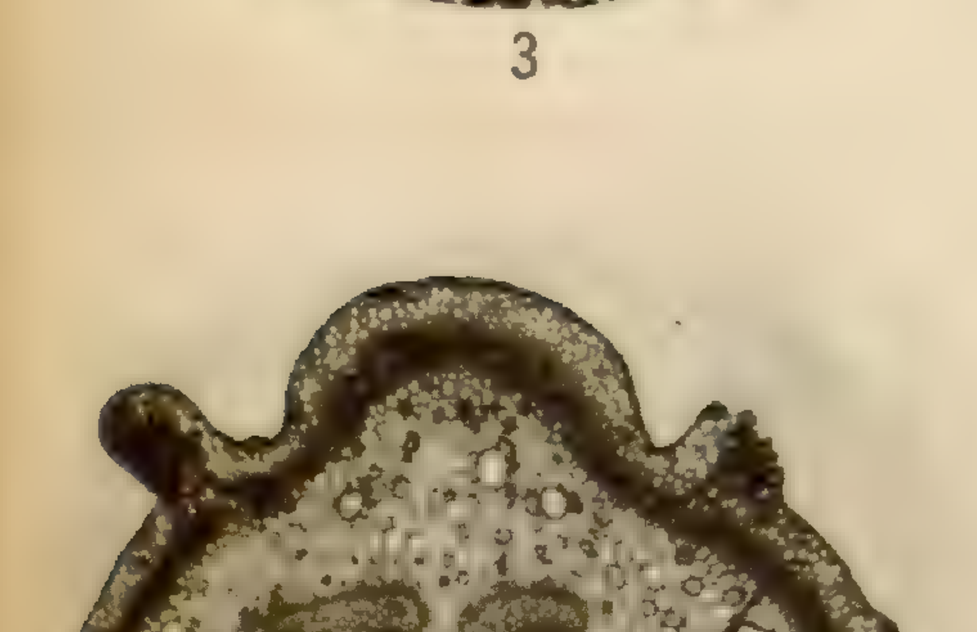

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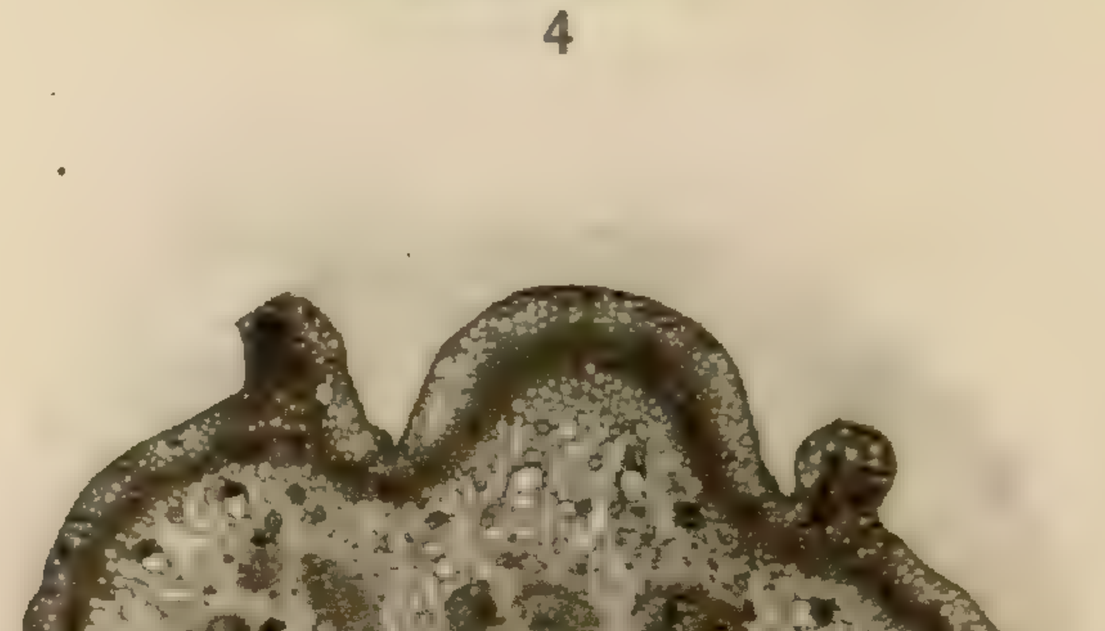

6

FERTILIZATION AND EMBRYOGENY IN DIOON EDULE[1]

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 141

CHARLES J. CHAMBERLAIN

(WITH PLATES XIV–XVII)

Fertilization in *Dioon edule* occurs from the second week in April to the second week in May. I have not been able to visit Mexico at this season of the year, but through the kindly influence of Gov. TEODORO A. DEHESA, who for several years has aided me in my investigation of Mexican cycads, and through the constant co-operation of Mr. ALEXANDER M. GAW, of the State Bureau of Information, Xalapa, Mexico, I have been able to secure material as regularly as if I had lived at Chavarrillo, where *Dioon edule* is most abundant. In cones picked at Chavarrillo, April 10, 1905, and examined at Chicago, April 21, nearly every nucellus contained one or more pollen tubes in which sperms were swimming vigorously; the next day there were not so many, and three days later nearly all pollen tubes had discharged their sperms; but as late as May 10 a few sperms were found. Consequently it would be possible for fertilization to occur at this late date, although not very probable, for all eggs capable of fertilization would probably have been fertilized already. A large cone picked at Chavarrillo, April 16, 1910, and examined at Chicago seven days later, contained embryos four times as long as the archegonia; consequently fertilization must have occurred as early as April 7. A few embryos in this cone were still in the free nuclear stage, but no pollen tubes were seen. These cones indicate the limits of the fertilization period as observed in the collections of six seasons. April 15 may be regarded as the optimum time, with fertilization frequent a week earlier and a week later, but becoming rare beyond these limits.

While fertilization may be somewhat delayed in cones sent to such a distance, the processes must be normal, for embryos

[1] Investigation prosecuted with the aid of a grant from the Botanical Society of America.

develop up to the cotyledon stage even in cones from which most of the sporophylls have been removed in securing material. In cones which arrive in Chicago with embryos in early cotyledon stages, the development is completed perfectly and the seeds will germinate.

Fertilization

The relations of the various structures at the time of fertilization are shown in fig. 1. The outer fleshy coat of the ovule has become highly differentiated, with its epidermal and hypodermal layers and deeper tissues containing tannin cells, mucilage ducts, and the outer vascular system. The stony coat has become so hard that it is difficult to cut it with a strong pocket knife; in fact, material of this and later stages was secured by sawing the ovule transversely with a fine saw. The inner fleshy coat has been reduced to a thin, papery membrane which, in the figure, appears as a dark border lining the inner surface of the stony layer. The nucellus, with its conspicuous beak and pollen tubes, has begun to sag. The tissue of the female gametophyte has become quite firm and contains numerous tannin cells, while the archegonial chamber has reached its maximum depth, and the nucleus of the central cell of the archegonium has just divided to form the ventral canal and egg nuclei. As stated in the paper on spermatogenesis in *Dioon edule* (8), the archegonial chamber is moist but contains no liquid before the pollen tubes begin to discharge. The sperms in escaping through the rather small rupture in the end of the pollen tube—there is no pit or pore—are much constricted, but soon regain their form and begin to swim. The amount of liquid discharged by a single pollen tube is small in comparison with the size of the archegonial chamber, and if the liquid should spread evenly, it would not be sufficient to cover the sperms; however, it behaves somewhat like a drop of water on a greasy surface, not spreading much, but moving until it comes into contact with the neck of an archegonium. The sperms move vigorously after being discharged from the pollen tube, but how long they might continue to swim under natural conditions in the archegonial chamber could not be determined. I had little success in keeping them alive in sugar solutions. When a sperm comes

into a sugar solution, the nucleus often slips out from the cytoplasmic sheath, and the cytoplasm then rinses off from the spiral band, leaving the band with its cilia almost free from any cytoplasm.

Before the pollen tubes have begun to discharge, the megaspore membrane over the archegonia has been ruptured, so that there is no obstruction between the sperms and the necks of the archegonia.

What causes the sperm to enter the egg? The classical experiments on chemotaxis would suggest a solution, but there is no free open passage as in bryophytes and pteridophytes, in which the small sperms may move freely in response to a slight stimulus. On the contrary the neck is closed, and the sperm becomes greatly constricted while entering, so that, whatever the force may be, it is a very strong one. Against the theory that chemotaxis is responsible for the movement, it must also be remembered that so skilful an investigator as MIYAKE (**5**) was unable to detect any chemotactic response when studying the sperms of *Cycas revoluta*, although he used the solutions which are uniformly effective with the sperms of pteridophytes, and in addition used the squeezed-out contents of the *Cycas* eggs.

It is well known that in many algae a small portion of the contents of the egg is extruded just before fertilization, a passage to the egg being facilitated in this way. In *Dioon*, just before fertilization, numerous preparations show a little protoplasm about the necks of the archegonia, and for a long time I assumed that it had been squeezed out from the egg by the pressure of the knife as the square block containing the archegonia was being cut out from the top of the endosperm before fixing. It was also noted that when material near the fertilization period is dropped into water or the fixing agent, a small bubble appears at the neck of the archegonium. The drop of liquid from the pollen tube has a very high osmotic pressure, and when it comes into contact with the extremely turgid neck cells, these lose so much of their contents that, in preparations, they appear more or less plasmolyzed. The pressure within the egg has been increasing until the contents are retained only by the rigidity of the turgid neck cells, and consequently even a slight decrease in turgidity of the neck cells would allow the escape of a small portion of the cytoplasm of the upper part of the egg, together,

probably, with some gas. In this way there is formed at the apex of the egg a vacuole, which may be of very short duration. In the absence of more definite knowledge, we suggest that this series of conditions would result in drawing the sperm into the egg, the cilia merely keeping it oriented, for sperms just within the egg showed the apex in advance in every case observed. It has already been noted in the paper on spermatogenesis (8) that the sperms have an amoeboid movement in addition to the movement by cilia. This amoeboid movement doubtless facilitates the entrance into the egg.

While the whole sperm enters the egg, the nucleus soon slips out from the cytoplasmic sheath and moves toward the egg nucleus, leaving the sheath with its ciliated band in the upper part of the egg. It may be that the constriction of the sperm during its entrance into the egg loosens the sheath from the nucleus so that it slips out more readily, for projections of various sizes extend from the nucleus into the sheath, and these would naturally become loosened. When more than one sperm enters the egg, it is worth noting that the nucleus of the second sperm does not slip out from the sheath, but remains intact in the cytoplasm at the top of the egg, where it may be distinguished to rather late stages in the development of the proembryo. Doubtless the first sperm opened the neck of the archegonium, so that the second suffered little constriction and the cytoplasmic sheath was not loosened. In some cases, at least, the sperm is still capable of vigorous movement after it is within the egg, as may be seen in fig. 1, where the contents of the egg have been stirred by the vibration of the cilia.

The cytoplasm of the sperm gradually mingles with that of the egg, and the two soon become indistinguishable, but the ciliated band maintains its identity much longer, and may be distinguished throughout the free nuclear development of the embryo, after which it becomes faint and finally merges with the cytoplasm of the upper part of the egg. As in *Zamia* (4), portions of the band occasionally penetrate farther, sometimes being found below the middle of the egg. The cytoplasm never surrounds the fusion nucleus, as in some gymnosperms, and there is no indication that it exerts any active influence upon the egg. That it does not stimulate is

evident from the fact that development is weakest in the upper portion of the egg.

The nucleus of the sperm enlarges somewhat during its passage to the egg nucleus, but details in the changes in its chromatin and changes in the chromatin of the egg nucleus were not studied. No preparation was secured which would show whether the chromatin contributions of the conjugating nuclei are distinct, as in *Pinus*, or whether the nuclei fuse in the resting condition, as is claimed for some gymnosperms. For a study of the nuclei at the time of fusion, *Ceratozamia* is a more favorable form, and consequently this feature will be investigated in that genus.

Embryogeny

HISTORICAL

The development of the cycad embryo has been studied in only two genera, *Cycas* and *Zamia*, and a few rather later stages have been noted in *Ceratozamia* and *Encephalartos*.

As early as 1877 WARMING (1) described some of the later stages in the development of the embryo of *Ceratozamia*, but in all cases the embryo had already passed through the base of the egg and invaded the endosperm. He noted the long suspensor and particularly the single cotyledon, a feature which Sister HELEN ANGELA (6) has since proved to be due to gravity, the missing cotyledon always appearing when developing seeds are rotated on a klinostat.

TREUB'S account of *Cycas circinalis* (2) in 1884 was comparatively full. A prolonged period of free nuclear division results in the formation of numerous free nuclei which are crowded to the periphery by a large central vacuole. Wall-formation then begins and the embryo, with its long suspensor, is organized from the cells at the base of the proembryo.

IKENO'S (3) account of *Cycas revoluta* confirms TREUB'S except in regard to the formation of the vacuole. IKENO finds that a large number of small vacuoles appear in the cytoplasm of the central portion of the egg, and that this central portion with its contained nuclei then disorganizes, leaving a parietal layer of protoplasm and nuclei, while a single large vacuole occupies the

center. After this stage, there are a few free nuclear divisions at the base of the egg before walls begin to appear, and at the same time amitotic divisions may take place in the upper portion.

COULTER and CHAMBERLAIN (4) found in *Zamia floridana* a somewhat different condition. After about eight simultaneous free nuclear divisions, giving rise to 256 free nuclei, walls appear at the base of the proembryo, just as in the formation of endosperm in most angiosperms, but no vacuole is developed.

SAXTON (9) has recently described some of the later stages in the embryo of *Encephalartos*. He finds that the suspensor is a root cap, and that the embryogeny is very similar to that of *Ginkgo*.

DIOON; FREE NUCLEAR PERIOD

In *Dioon edule* fertilization is followed immediately by a long period of simultaneous, free nuclear division. The first mitosis of the fusion nucleus occurs in the position where fertilization has taken place, a little above the middle of the egg, the spindle being oblique, as is usually the case in gymnosperms. The succeeding mitoses follow rapidly, and the nuclei, even as early as the 16-nucleate stage, become rather evenly distributed throughout the entire proembryo. Occasionally the nuclei move toward the bottom of the proembryo, the 16, 32, and 64-nucleate stages having been found with all the nuclei below the middle of the proembryo, and in one case a 64-nucleate stage had all the nuclei in the lower third. On the other hand, two 4-nucleate stages were observed with all the nuclei above the middle of the proembryo.

In stages following the 64-nucleate stage—resulting from the sixth mitosis—the number of nuclei in the lower part of the proembryo is likely to be considerably larger than that in the upper part. At the 128 and 256-nucleate stages—resulting from the seventh and eighth mitoses—the larger number at the bottom is due to a settling of the nuclei; but at the ninth mitosis some of the nuclei in the upper half of the proembryo may fail to divide, and thus add to the disproportion. It may happen, occasionally, that the ninth mitosis, which gives rise to the 512-nucleate stage, may be the last of the simultaneous divisions; but usually there is a tenth mitosis, which would give rise to 1024 nuclei, if all nuclei

should divide at every simultaneous mitosis. A rough estimate, based upon fig. 6, shows that the evanescent walls, to be described later, are those resulting from the tenth mitosis; and fig. 7, in which permanent walls have been established, shows that in this proembryo the permanent walls appeared in connection with the tenth mitosis. We have not found any case which would indicate an eleventh mitosis, and only a few cases where permanent walls seem to have been formed at the ninth mitosis; while nearly all proembryos in approximately the stage shown in fig. 7 indicate that there have been ten mitoses with permanent walls beginning in connection with the tenth.

During the period of free nuclear division, the figures are entirely intranuclear and are characterized by the abundance and persistence of the spindle fibers (figs. 2–4). The nuclear membrane is formed quite late (fig. 3), but when once formed it becomes unusually thick, and pieces of it may be seen until late prophase or early metaphase of the next mitosis (fig. 2, *n*).

DIOON; EVANESCENT SEGMENTATION

The most characteristic feature of the proembryo of *Dioon edule* is the complete but evanescent segmentation of the entire egg. In one case, as early as the 64-nucleate stage, faint walls were observed dividing the entire proembryo into uninucleate cells. Such walls break down completely before the next mitosis begins. At the seventh and eighth mitoses, giving rise to the 128 and 256-nucleate stages, the appearance of walls is more frequent and they break down less rapidly; while at the ninth mitosis, giving rise to the 512-nucleate stage, the walls are probably always formed; and at the tenth division the walls are formed; but while they disappear in the upper portion of the proembryo, leaving it in free nuclear condition, they persist at the base, constituting the first permanent walls. As soon as the proembryo becomes cellular, the simultaneous mitoses are succeeded by the scattered mitoses which one expects in a young cellular embryo.

The evanescent walls consist of broad bands of spindle fibers, about two-fifths of the spindle nearest the daughter nuclei disappearing very early, while the middle fifth remains long enough to

cause a segmentation which is so conspicuous that it is seen easily with a pocket lens (figs. 5, 6).

The evanescent walls were, for a time, the most puzzling feature in the embryogeny, especially while it was thought that they belonged exclusively to some particular mitosis. As observations multiplied and it became evident that the evanescent segmentation might occur at the sixth mitosis and was increasingly frequent at the seventh, eighth, and ninth mitoses, the explanation became evident. The early mitoses, up to the sixth, follow in such rapid succession that a new mitosis is begun before the preceding one could establish a wall. Between the succeeding mitoses the intervals are increasingly greater, and consequently the natural tendency of a spindle to develop a wall finds a more marked expression.

We regard the appearance of evanescent walls as a reversion, indicating that the ancestors of *Dioon* had embryos which were cellular throughout. It can hardly be questioned that the free nuclear condition in gymnosperms, whether in the proembryo or in the gametophyte, is not a primitive but rather a highly specialized condition. In the small eggs of the pteridophytes, including even the heterosporous genera, the first nuclear division is followed by the formation of a wall. We suggest that free nuclear division in the proembryo of gymnosperms arose in connection with the increasing size of the egg, the increased mass of the egg becoming too large to be segmented, and at the same time the large mass favoring rapidly succeeding mitoses. The nuclei divide simultaneously because exposed to practically similar conditions. As mitosis continues and the mass of cytoplasm about each nucleus becomes less, the mitoses succeed each other less rapidly, and as the relation between the nuclei and surrounding cytoplasm approaches that which is found in the ordinary tissues, segmentation begins. If this view is correct, we should expect the most extensive free nuclear periods in the largest eggs, and such is certainly the case. The egg of *Dioon edule* often reaches a length of 5 mm., and the number of free nuclei is about 1000, theoretically 1024. *Zamia*, with an egg about 3 mm. in length, has 256 free nuclei; and *Gingko*, with an egg of somewhat approximately the

same mass, shows the same number. The much smaller eggs of Coniferales have comparatively short free nuclear periods, showing only 32, 16, 8, 4, and 2 free nuclei; while in the small egg of *Sequoia* the first mitosis is followed by a wall.

While it might be tempting to regard this as a reduction series, and to regard forms with a large number of free nuclei as primitive, it seems probable that the number of free nuclei is correlated merely with the size of the egg. That the large number does not prove antiquity is shown by the fact that *Dioon* has 1000 free nuclei, while *Pinus* has only 8 (i.e., walls appear in connection with the 8-nucleate stage), and yet *Pinus* is much more ancient than *Dioon*. We should expect to find the critical forms among the lower Cycadofilicales as they began to be differentiated from some heterosporous fern ancestry. These forms, which are still to be discovered, should have small eggs with complete segmentation not preceded by any free nuclear period, the free nuclear feature appearing later in connection with an increased size of the egg. Although this is highly theoretical, we believe that it suggests an explanation of the structures as we find them in living gymnosperms.

DIOON; THE CELLULAR EMBRYO

At the last mitosis of the free nuclear or evanescent segmentation period, permanent walls are developed at the base of the proembryo, the walls in the upper part being evanescent and disappearing as before. The nuclei in this upper region do not divide any more and many of them disorganize. In the basal region nuclear division, always accompanied by cell division, progresses rapidly; and while one can still estimate with some degree of exactness the extent to which the free nuclear stage has progressed, a small-celled tissue is formed (fig. 7). At the stage shown in this figure, there is practically no indication of regions corresponding to the "rosette," suspensor, and embryo proper regions of many conifers. At this stage the archegonium jacket is still conspicuous, and at the base of the proembryo the jacket has become extended into a tissue several cells deep, contrasting sharply with the adjacent starchy cells of the endosperm. Cellulose walls have formed on the peripheral surfaces of the cells of this proembryo and the egg membrane is still intact.

Very soon after the stage shown in fig. 7, a differentiation becomes apparent. A thick wall forms a sort of diaphragm between the definitely cellular and the free nuclear or loosely cellular portions of the proembryo (figs. 8, 9, *d*). Just below the diaphragm the cells are large and with scanty protoplasmic contents, while one and in the middle two layers of cells are much smaller and have dense protoplasmic contents (fig. 8). This more deeply staining region at the tip becomes the embryo proper, while the large cells, in contact with the diaphragm, will differentiate into the suspensor. Long cells like *a* and *b* in fig. 8 may divide again, the outer cell then contributing to the suspensor, while the other forms a part of the "rosette" and never gets beyond the original limits of the egg. The suspensor cells now divide both longitudinally and transversely, and it becomes difficult or impossible to distinguish any boundary between suspensor and embryo proper (fig. 9). As the periclines at the tip of this figure indicate, the dermatogen has not yet been differentiated. In both figs. 8 and 9 the embryos have not yet pierced the egg membrane.

The egg membrane now disorganizes, apparently becoming digested, and the rapidly elongating suspensor thrusts the embryo through the base of the egg into the endosperm. At this time mucilage ducts begin to appear in the suspensor (fig. 10). As soon as the embryos break through the egg membranes, the four or five or six suspensors become twisted together, and as one dissects them out they appear like a single suspensor with one embryo at the tip; but when they have reached a length of 1 cm., a careful examination with a pocket lens will show unsuccessful embryos at various distances from the egg region and a single embryo at the tip. I have never seen a suspensor branching, as described for *Encephalartos* by SAXTON (**9**), but have seen unsuccessful embryos which project somewhat from the general suspensor and so caused the appearance of branching.

The suspensor is a remarkable feature of the cycad embryo. Its growth and twisting is accompanied by an extensive disorganization of the endosperm in the archegonial region, especially just beneath the archegonia, so that there is formed a large cavity which becomes filled with the long suspensor. The cavity is moist,

but not full of liquid. The cells disorganized in the formation of the cavity must have contributed largely to the growth of the suspensor, since the embryo itself is receiving from surrounding cells enough to account for any increase in its size. That the suspensor exerts a vigorous thrust is evident from the fact that when released it relaxes like a spring which has been under tension. The suspensor when stretched out reaches a length of 75 mm. As the embryo matures, the suspensor does not disorganize, but remains as a tough dry thread, strong enough to lift the weight of the entire embryo.

The embryo develops rapidly, cell division taking place throughout the entire embryo, while the suspensor cells elongate and also occasionally undergo mitosis (figs. 10–12). In the last figure the two upper mitoses are in the suspensor and the three lower in the embryo proper. It is interesting to note that such mitoses are found in cones which have been taken from the plant in southern Mexico, shipped to Chicago in a basket, and after arriving have been lying on the laboratory table for two or three weeks.

The first indication of any differentiation of the embryo proper is the appearance of increased vigor in cell division in the region just below the suspensor, indicated by *x* in fig. 14. This region, which appears in the embryo and not in the suspensor, is the beginning of the coleorhiza, an organ which rapidly becomes conspicuous and soon constitutes the largest part of the embryo (figs. 15, 16).

While the coleorhiza and the root cap are spoken of as two organs, and while they differ widely in general appearance, in cell structure and in function they are morphologically only one organ, the root cap. The coleorhiza at first consists of thin-walled cells with numerous large starch grains, but toward the close of the intraseminal period the cell walls become very hard and thick, so that the term coleorhiza is quite appropriate. Just within the coleorhiza the mature embryo shows a cone of thin-walled cells, rich in tannin, derived from the same meristem, the beginning of which is seen in fig. 14. These cells are the outer layers of the root cap. At germination the pressure is developed, at least in large part, by the activity of the meristem which is adding new

layers to the root cap. The pressure, crowding the coleorhiza against the micropylar end of the seed, causes an irregular jagged fracture of the stony coat of the seed, through which the embryo emerges. It is only after the fracture is large enough to permit the exit of the embryo that the root cap pierces the central portion of the coleorhiza, the thick-walled cells of which may be seen clinging to the root in threadlike masses even after the axis of the seedling has become vertical.

The late differentiation of body regions is a noticeable feature of the cycad embryo. At the stage shown in fig. 15, not only is the differentiation into periblem and plerome still incomplete, but even the dermatogen is not yet differentiated, as may be seen by the periclines in the cotyledons and especially in the stem tip (figs. 15, 17). Perhaps the importance of division by anticlines only has been overestimated, for in this embryo the outer layer looks like a dermatogen long before the periclines cease to appear.

A general view of an embryo at the stage shown in fig. 15 may be seen in the accompanying diagram (fig. 16), drawn from the same preparation. Just below the suspensor with its large mucilage cavities is the swollen coleorhiza. Starch is found in the suspensor, but is most abundant in the peripheral and lower regions of the coleorhiza. Cell division is most active in the dotted region of the stem tip. While the general appearance of the mitoses is very different from that described for the free nuclear period, it is probable that the difference is not so great as it seems, for in fig. 18 the spindle may mark the limit of the nuclear membrane.

A diagrammatic section through a ripe seed is shown in fig. 19. The embryo extends almost the entire length of the seed, the cotyledons constituting the principal mass. The first functional leaf, if drawn on a large scale, would show the primordia of pinnules, the scale leaves not showing such a differentiation. The outer fleshy layer and the middle or stony layer (shaded) are easily distinguished, but the inner fleshy layer, while forming a conspicuous membrane containing the inner vascular system, is too thin to be shown in the diagram. Although the stony layer is quite thin in the region of the pit at the base of the seed, the cotyledons never emerge at

that point, but remain in the seed, sometimes until the seedling is three or four years old.

The embryo may develop continuously, germinating without any resting period, or may germinate after a resting period. Seeds which had been in the laboratory for two years germinated readily, but how long they might retain their power of germination is uncertain.

While the general course of development in the later stages of the embryo is the same in all of my material (*Dioon*, *Ceratozamia*, *Zamia*, *Microcycas*, and *Encephalartos*), there are considerable differences in details which may prove suggestive, and consequently no more detailed description will be given until a comparative study has been made.

The development of the vascular system of the embryo and seedling of *Dioon edule* has been investigated in this laboratory by THIESSEN (**7**).

Summary

1. The liquid from the pollen tube causes a decrease in the turgidity of the neck cells, and this allows a portion of the upper part of the egg to escape, thus forming a vacuole at the top of the egg. The entire sperm is thus drawn into the egg.

2. There are sometimes nine, but oftener ten simultaneous free nuclear divisions, resulting in the formation of 512 or 1024 free nuclei.

3. There is a complete but evanescent segmentation of the entire proembryo, the walls then disappearing except at the base of the proembryo, where they become permanent.

4. The coleorhiza and root cap, although differing in appearance, cell structure, and in function, are formed from the same meristem, and both are morphologically root cap.

5. Plerome, periblem, and dermatogen are differentiated quite late in the development of the embryo.

6. The seed germinates without any resting period, but also has been germinated after a rest of two years.

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DESCRIPTION OF PLATES XIV–XVII

FIG. 1.—Upper part of ovule at the time of fertilization; the figure is reconstructed from several sections; the pollen tube on the left shows the body cell still undivided; the one in the middle shows two sperms and the remains of the stalk and prothallial cells; next to this tube is one in which the body cell has just divided, and the prothallial and stalk cells are still turgid; two pollen tubes which have discharged their contents are also shown; the dark line below the outer part of the nucellus is the megaspore membrane.

FIG. 2.—Late prophase during the free nuclear division in the proembryo, showing the intranuclear membrane (*n*). ×480.

FIG. 3.—Early telophase during the free nuclear period; the nuclear membrane has not yet been formed. ×480.

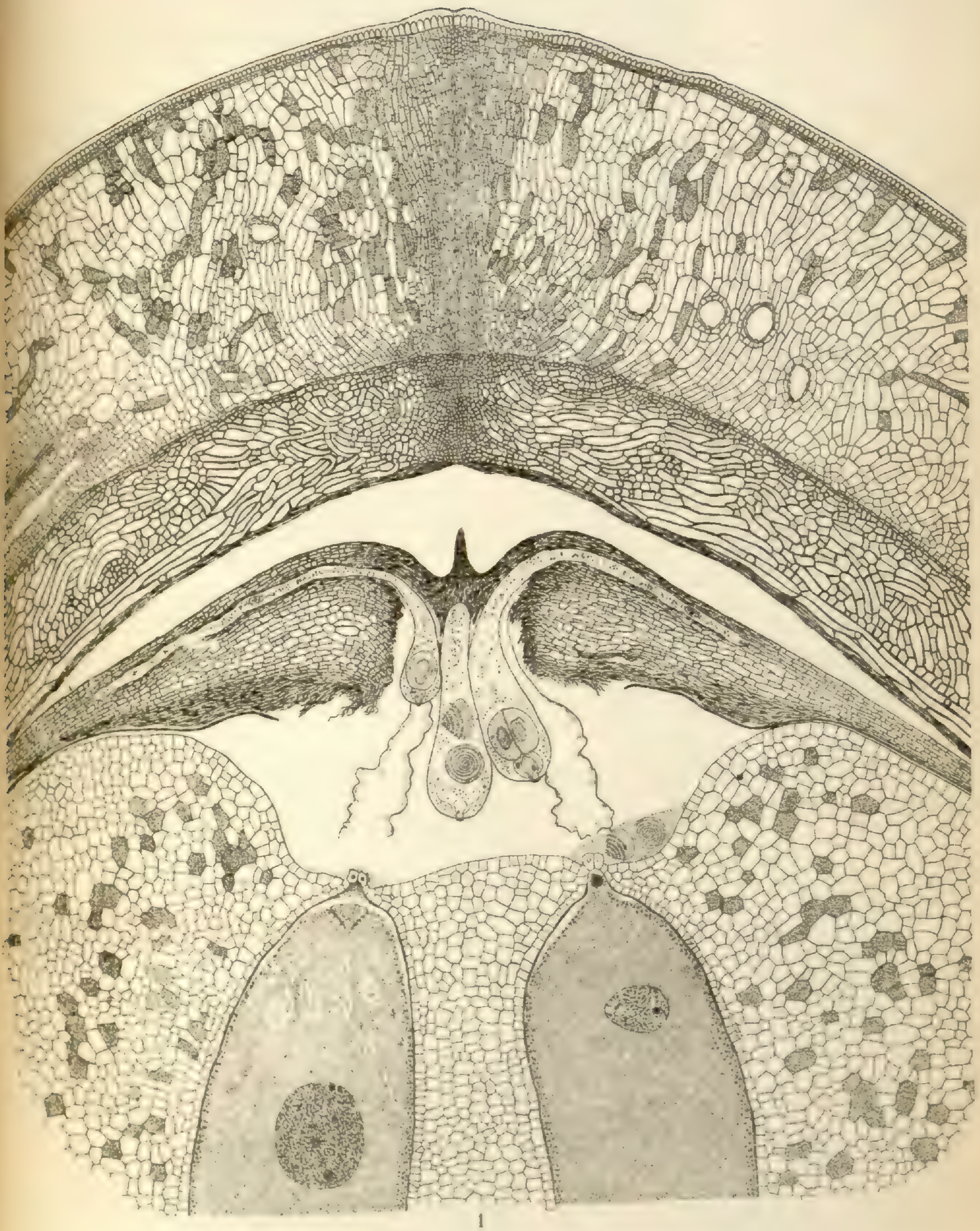
FIG. 4.—Telophase during free nuclear period; the central portion of the fibers from the evanescent walls. ×480.

FIG. 5.—Lower part of proembryo, showing evanescent but complete segmentation.

FIG. 6.—Diagram showing the complete proembryo of which fig. 5 shows only the lower part.

FIG. 7.—Lower part of proembryo, showing permanent walls at the base.

FIG. 8.—Young embryo: *d*, diaphragm; *f*, free nuclei; *a* and *b*, cells which may contribute to both "rosette" and suspensor.



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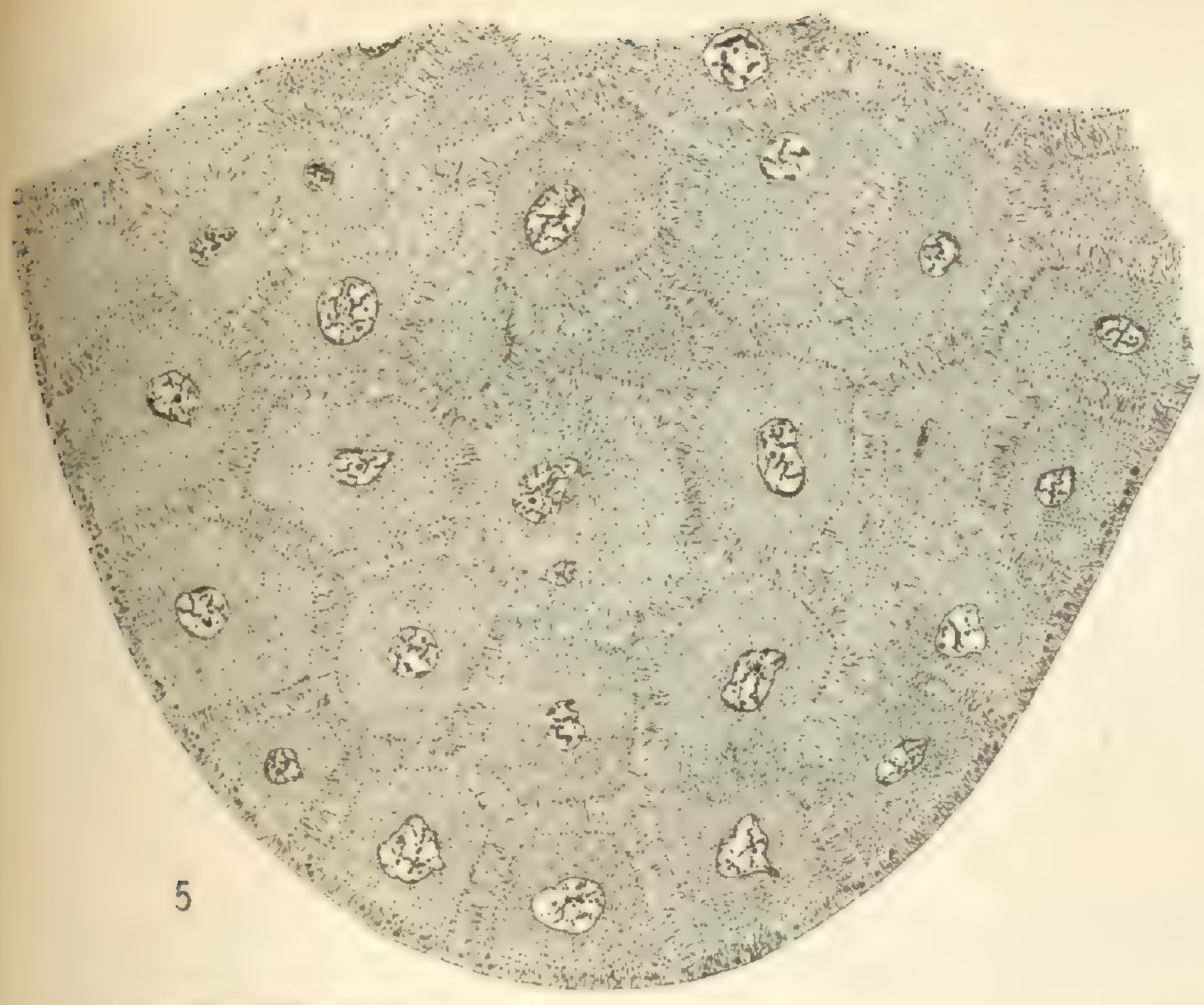

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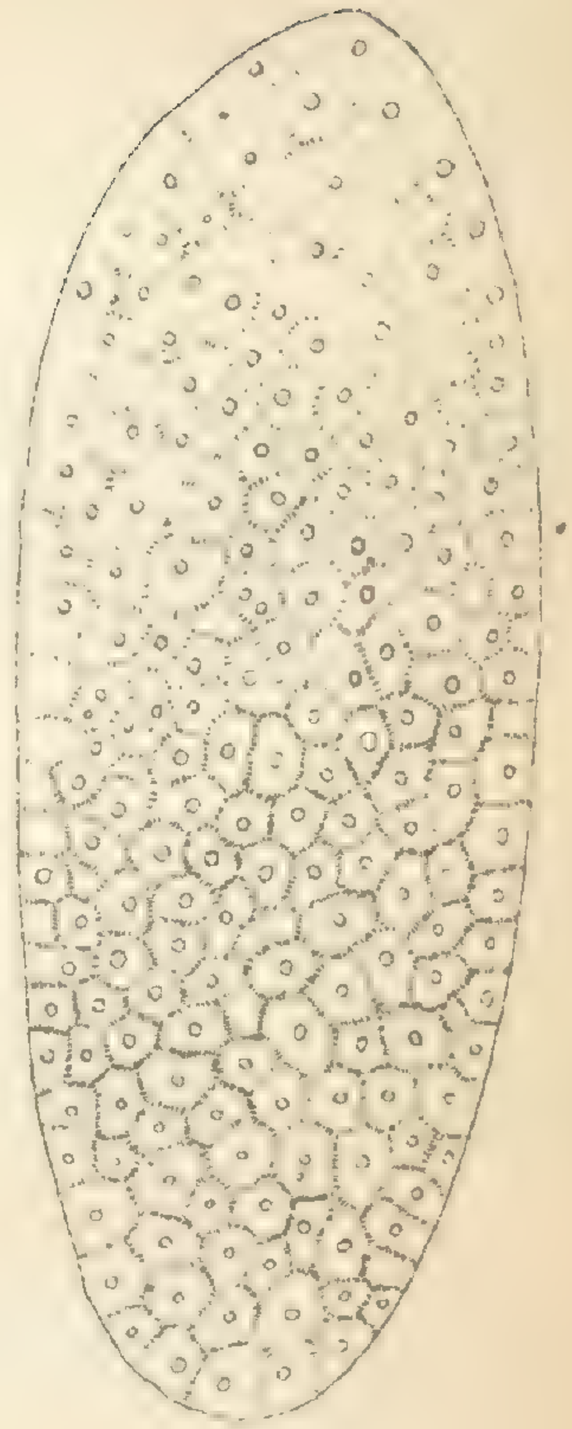

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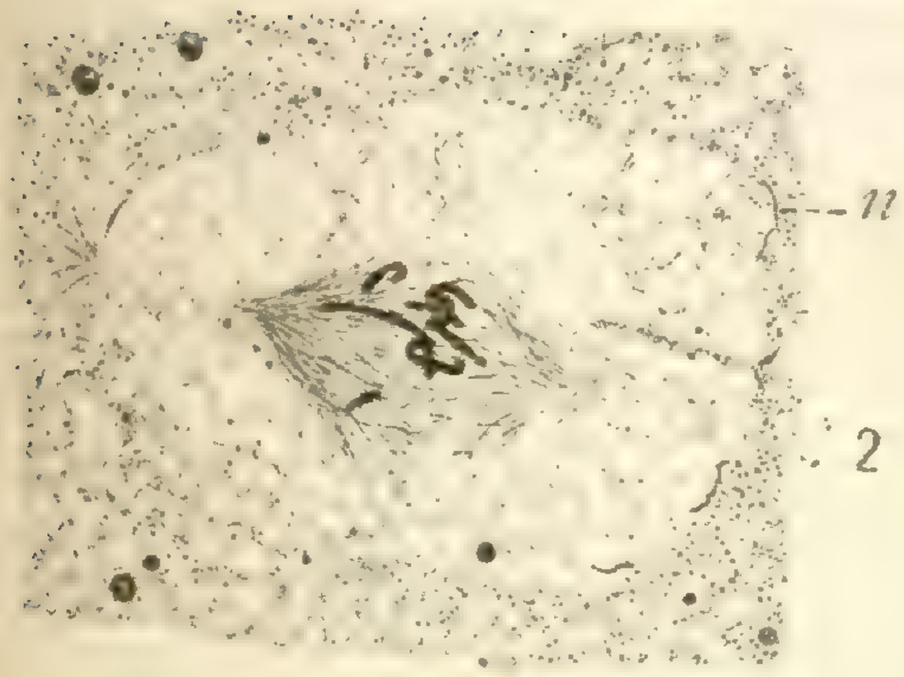

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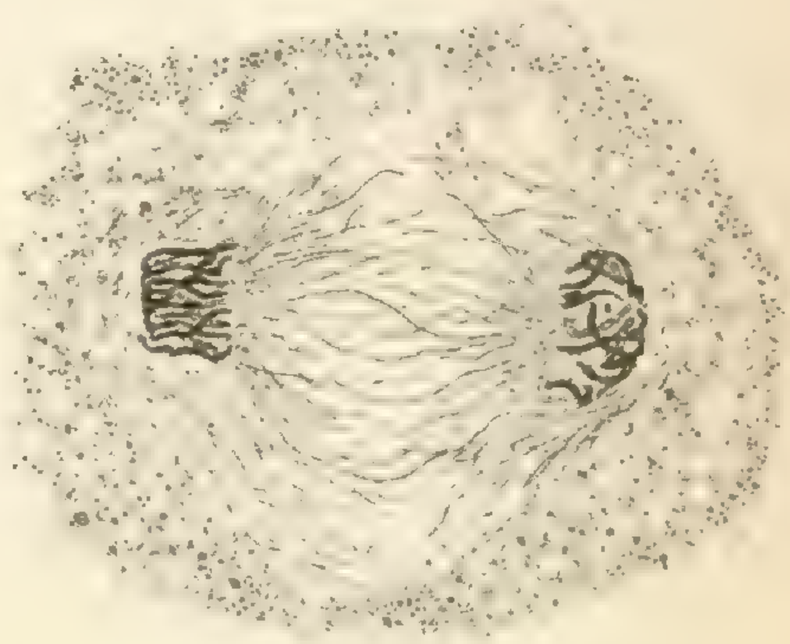

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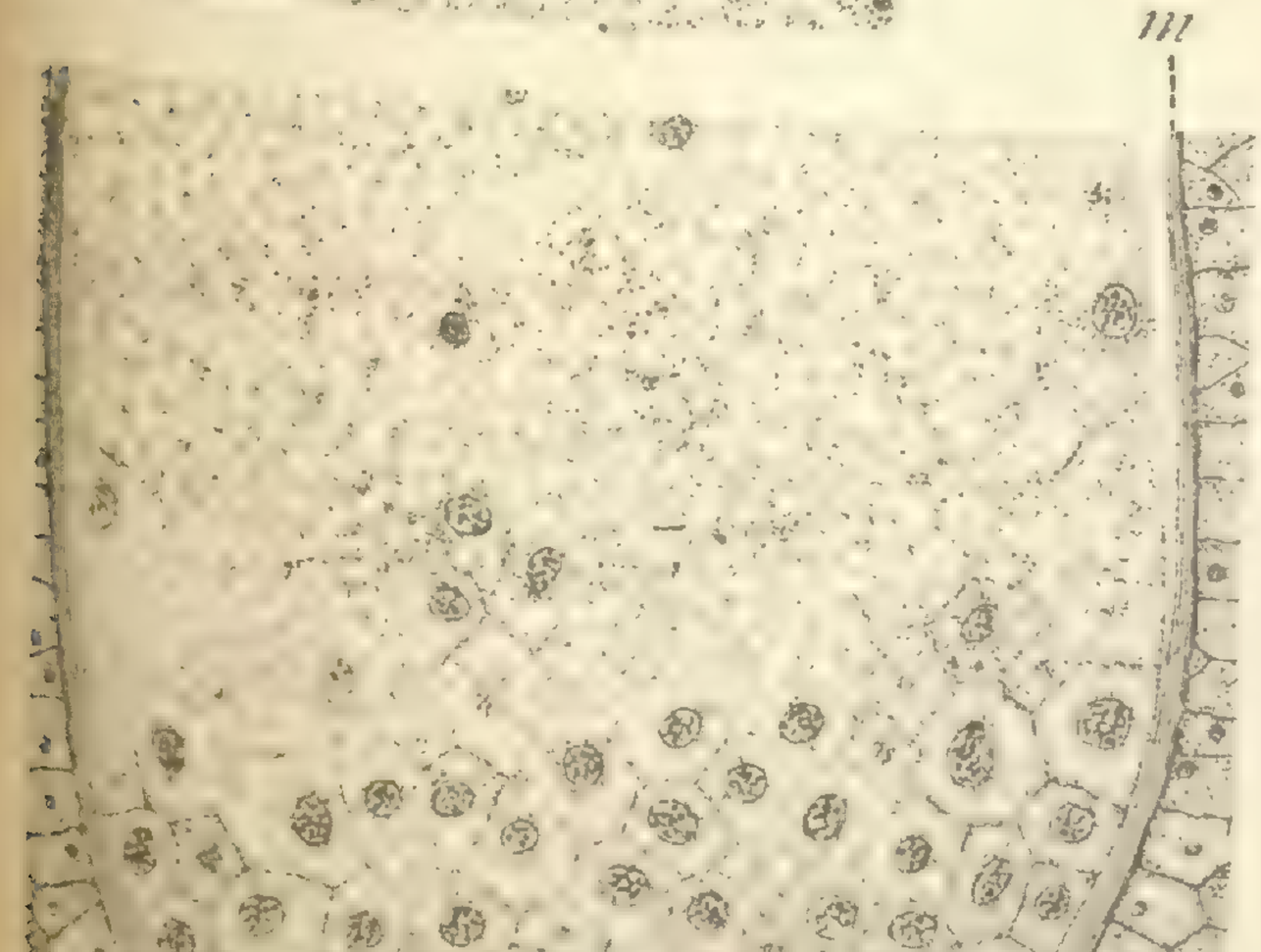

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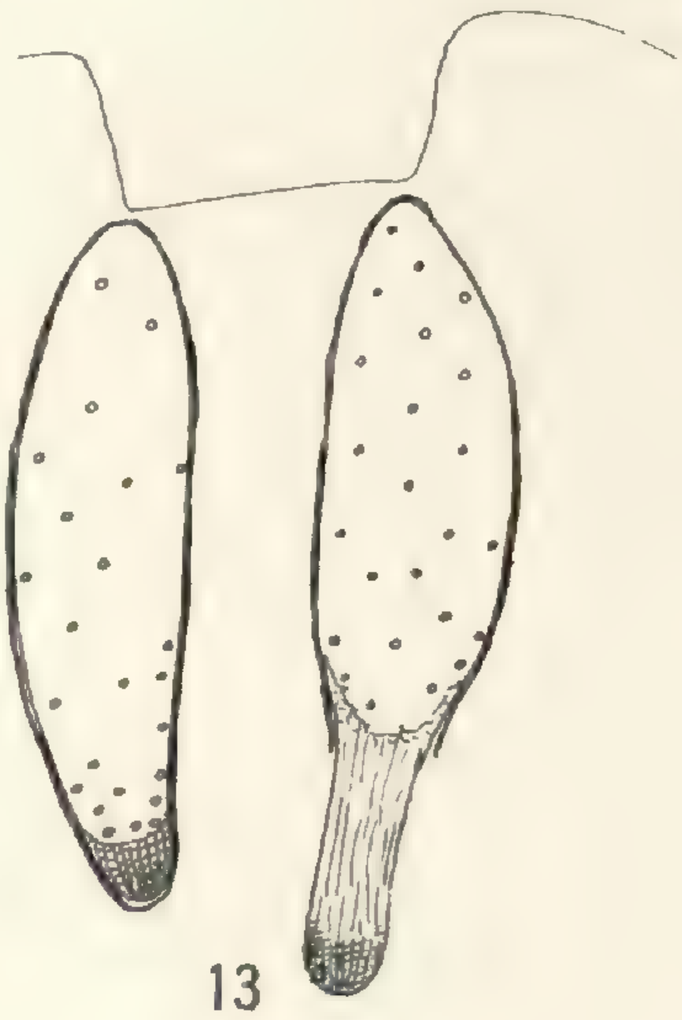

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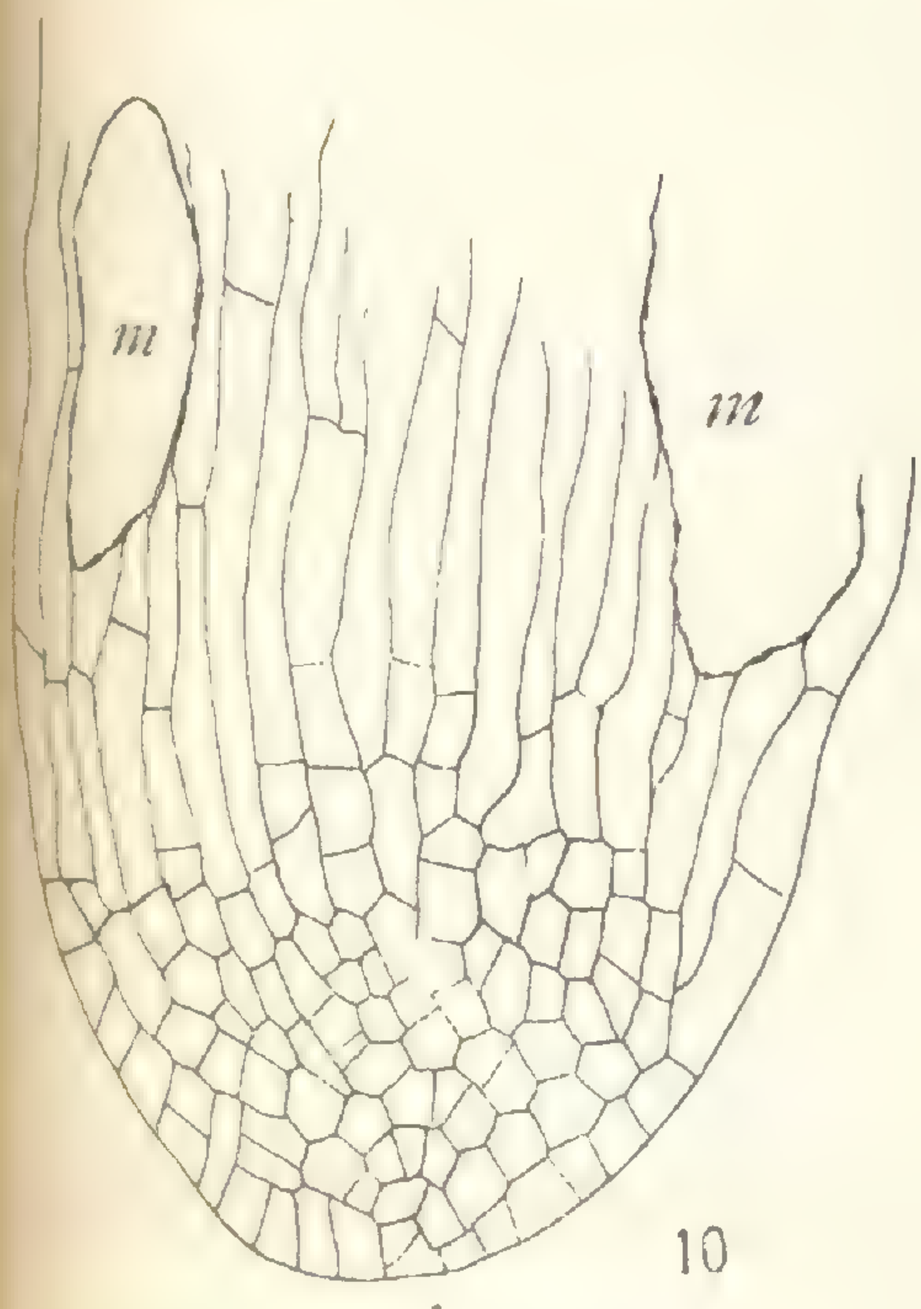

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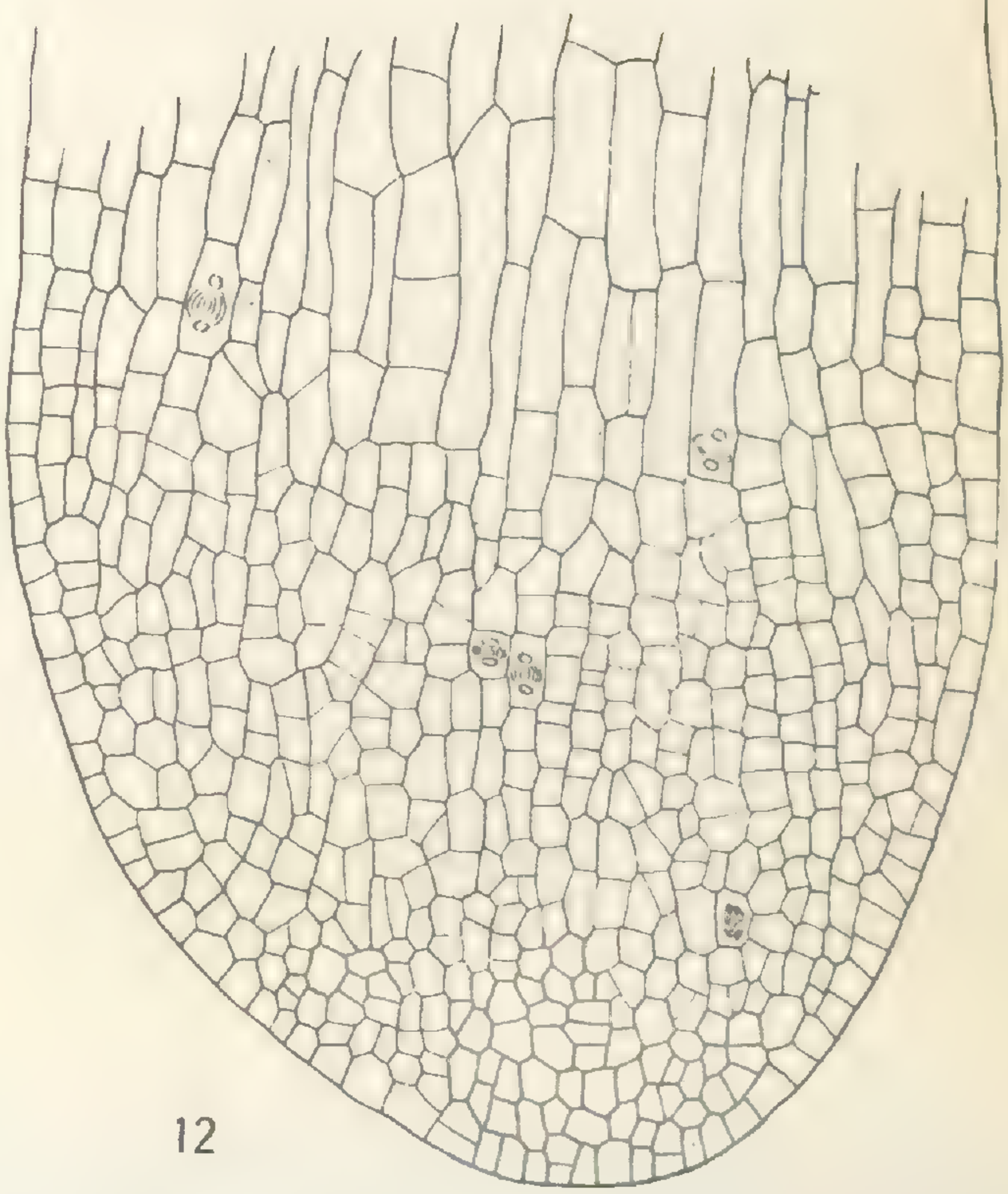

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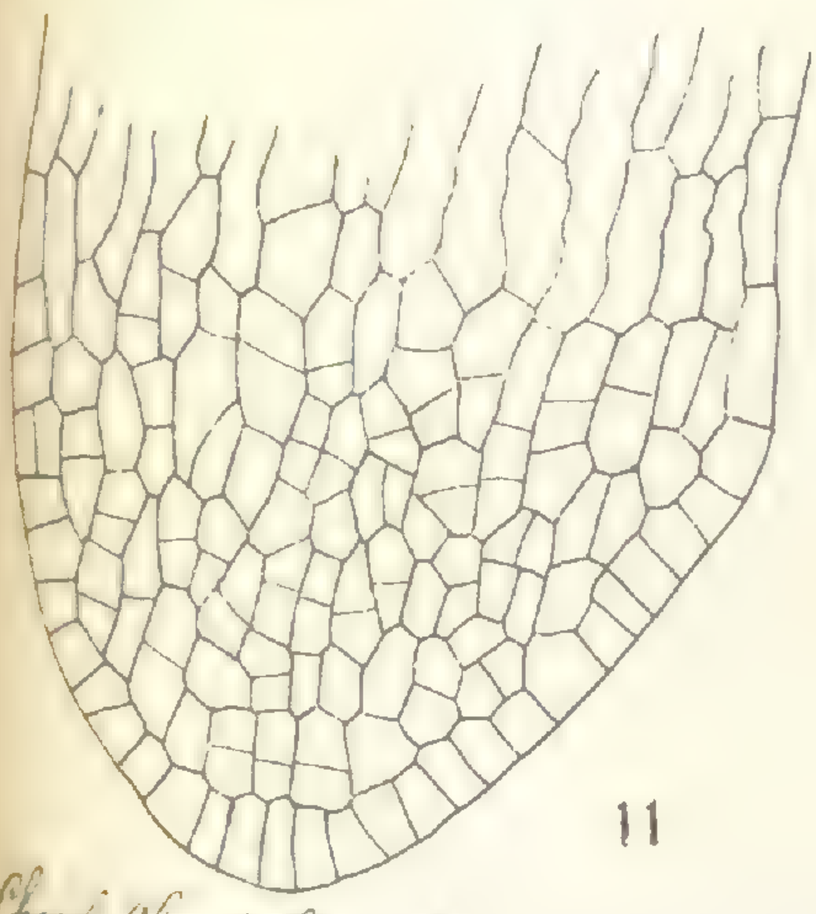

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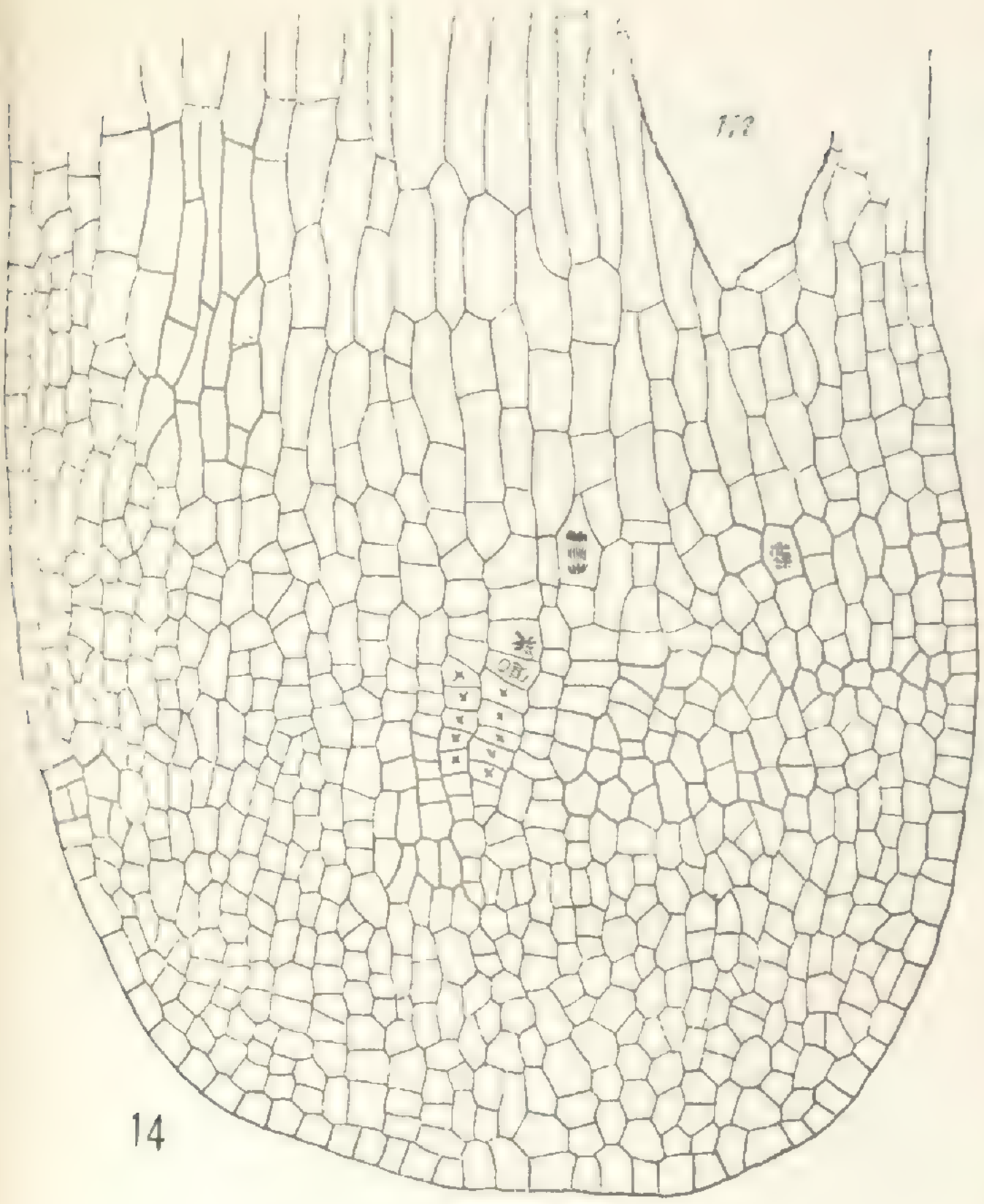
CHAMBERLAIN on DIOON



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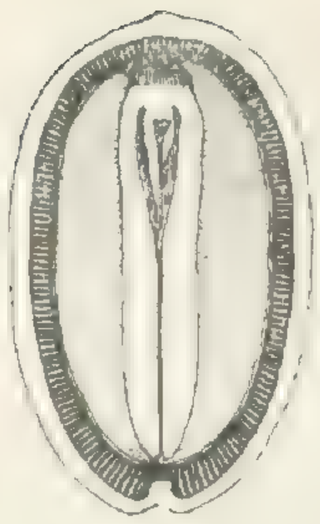

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Chas J. Chamberlain del.

CHAMBERLAIN on DIOON

FIG. 9.—Later stage, just before the embryo breaks through the base of the egg; the proembryo at the left in fig. 13 is in this stage.

FIG. 10.—Embryo after the suspensor has begun to elongate: *m*, mucilage cavities; the proembryo at the right in fig. 13 is in this stage.

FIG. 11.—A somewhat later stage.

FIG. 12.—Embryo shortly before the differentiation of cotyledons.

FIG. 13.—Diagram showing the topography of embryos at the stages shown in figs. 8–12.

FIG. 14.—Embryo showing the beginning of the meristem which is to produce the coleorhiza and later the root cap: *x*, the meristem; *m*, mucilage cavity in the suspensor.

FIG. 15.—Early cotyledon stage; the broader portion back of the cotyledons is coleorhiza; the periclines show that the dermatogen is not yet differentiated.

FIG. 16.—Diagram of the stage shown in fig. 15: *t*, suspensor; *c*, coleorhiza; *m*, mucilage cavity; the cells of the dotted region (*s*) are rich in starch; the cells of the dotted region at the stem tip are small, but slightly vacuolate and contain numerous figures.

FIG. 17.—Portion of the outer layer at the stage shown in fig. 16, showing that periclines are still taking place and that consequently the dermatogen is not yet differentiated.

FIG. 18.—Mitotic figure in the suspensor, showing rounded poles of the spindle.

FIG. 19.—Ripe seed, showing embryo with long cotyledons, the first leaf at the left, a scale leaf at the right, the coleorhiza (shaded), the stony layer (shaded), the outer fleshy layer, and the inner fleshy layer represented only by a fine line.

NOTES ON CHILEAN FUNGI. I

CONTRIBUTIONS FROM THE CRYPTOGAMIC LABORATORY OF HARVARD UNIVERSITY, LXVI

ROLAND THAXTER

(WITH PLATES XVIII AND XIX AND ONE FIGURE)

During the months of February and March 1906, it was my good fortune to pass six weeks of the antarctic summer and early autumn in the town of Punta Arenas, on the Straits of Magellan. These months being in many respects the most favorable for botanizing in this cold and wind-swept region, I had an excellent opportunity to become acquainted with its fungus flora, which was much richer and more varied than might have been expected, in view of the comparatively scanty phanerogamic flora and the general severity of the climate. Although for about a week in late February the mercury rose above 60° F. every day, and once even reached 70°, the mean diurnal temperature during the remainder of my stay was below 60°. Freezing temperatures were not uncommon, and it was not unusual in the morning to see the green beech forest on the hills to the west of the town loaded with snow. The small pools, in the localities where I collected, were often frozen over as late as the middle of the forenoon, while icicles might be seen hanging from flowers and grass growing on the dripping south slopes of the ravine which led to my usual collecting ground.

The town of Punta Arenas is not favorably situated as a base from which to make botanical excursions, since the whole shore of the Strait, as far as one can see to the south and for many miles to the north, has been devastated by fire; and the general aspect presented to the newcomer, as his steamer drops anchor in the open roadstead opposite the town, is to the last degree unattractive and forbidding. Formerly a superb forest of the antarctic beech (*Nothofagus*) covered the whole region, extending from the water's edge over a somewhat undulating plain, which gradually rises to the base of a range of hills or low mountains, the highest not

2000 feet above the sea, which form a wooded background for what is now a ghastly waste of dead trees still standing or fallen in confused heaps; and forming in many places, as one approaches the limits of the living forest, an almost impenetrable barrier.

Nearer the shore the dead trees have been largely cleared away, and the forest has given place to a firm turf which has taken possession in the vicinity of the town, and is grazed by divers domestic quadrupeds, so that there is no chance for reforestation. Over this area are scattered stunted specimens of the so-called varieties *bicrenata* and *uliginosa* of *Nothofagus antarctica*, some larger trees of the latter persisting in thin groves near the shore; while everywhere are clumps of "califate" bushes (*Berberis buxifolia*), associated with a flora of low annuals and perennials, which, though not very varied as to species and genera, is yet of the greatest interest to one unacquainted with its features.

The fungi occurring in connection with this coastal region are, like the flowering plants, for the most part different from those of the beech forest, and are more numerous than might have been expected, including a variety of striking forms. Among these the hexenbesen of the superb *Aecidium magellanicum*, to which it is my purpose to refer in a future note, are everywhere conspicuous on the califate, which harbors also several other rusts. Familiar forms are not altogether wanting, and *Psalliota campestris* grows in profusion over the turfy area, as well as a large puff ball which I took to be *Lycoperdon coelatum*. *Coprinus comatus* and *C. atramentarius*, entirely typical in appearance, were also occasionally seen about the town, and all of these formed a most welcome addition to the canned diet which prevails in these latitudes.

In order to reach the living forest where most of my collecting was done, it was necessary to traverse the coastal region above described: and this is most readily accomplished by following a narrow-gauge railroad which skirts the bed of the Rio de las Minas, traversing a portion of the deep gorge cut through the hills by this small stream, which, flowing from the west, empties into the Strait, after passing through the northern portion of the town. Even this broad ravine, which one enters somewhat abruptly after a tiresome walk of several miles against the biting wind which blows

almost without cessation from the west, has not been spared by fire, and its steep banks were capped by a skeleton forest; on the north more recently burned than elsewhere and carpeted for miles with fruiting *Marchantia*. It is thus not till one has passed the small coal mine from which the stream takes its name, and which forms the objective point of the railroad, that, after a walk of six or seven miles from the town, he finds himself in the living forest. Even here destruction of another kind was steadily progressing during my visit, and the lumberman's axe was rendering worse confounded the confusion already existing in the tangle of fallen trunks which seems to be characteristic of these woods.

When one considers that the trees composing this forest in the immediate vicinity of my collecting ground belong to only two species of a single genus, the variety of fungi which inhabit it is unexpectedly great. That a heavy forest of often very large trees should develop under such climatic conditions as have been described, is surprising; but that beneath its shade a considerable flora of the more fragile and perishable forms of fungi should develop, is even more difficult to understand. Yet here are found Amanitas, and other softer agarics, among which a very fine and large *Coprinus* is conspicuous, growing in masses from beneath fallen logs; Hymenogastreae are common and other soft hypogaeous forms, as well as Pezizae, Myxomycetes, etc., all flourishing and maturing in this valley; where, though the surrounding hills afford some shelter, the mercury can seldom rise much above 60° F., while freezing temperatures are common at night even in mid-summer, with frequent cold squalls of rain, hail, or snow. Although I made no special effort to collect them, I gathered about forty species of Myxomycetes, and I have never seen Hymenogastreae more abundant, in numbers of individuals at least. The more resistant forms of fungi were duly represented, especially the Pyrenomycetes; although the Polyporei, as elsewhere in the Chilean forests, were scanty, and here in bad condition. Of all these fungi, however, the most peculiar was the discomycetous *Cyttaria*, and the nearly spherical distortions of the esculent *C. Darwinii*, often reaching a diameter of several feet, were everywhere conspicuous on the trunks and branches, although I was too late to see in the

best condition the curious fructifications which sometimes hung by dozens from their under sides.

It had just rained heavily as I stepped into these dripping woods, and I shall not soon forget the first day that I passed in them amid almost a surfeit of new botanical sensations. Not only were the fungi for the most part entirely new to me, but the trees were covered with unfamiliar lichens. One small filmy fern was common; but, in marked contrast to the forests farther north, hepatics were not abundant or conspicuous, with a very few exceptions like *Lepidolaena magellanica*, which covered fallen logs in many places. Mosses were abundant, especially along the ravine, and in the woods about the mine I found the lovely *Dissodon mirabile* Cardot, growing in tufts on cow dung, often in company with *Tayloria Dubyi* Broth., and conspicuous from its large pearly-white hypophyses.

Apart from the rather meager gatherings brought back by the various expeditions which have visited the Magellan region, our knowledge of its fungi is largely due to the fruitful investigations of Professor CARLOS SPEGAZZINI, an active collector and keen observer, whose published papers on the fungus flora of Tierra del Fuego and southern Patagonia bear witness to the varied character of this flora even in a portion of the forest much farther south; and this, too, notwithstanding the fact that a large portion of his collections were lost by shipwreck. During my stay on the Straits, although my collecting grounds were very limited and the forest so difficult of access, I was able to recognize a considerable number of the forms described by SPEGAZZINI, as well as certain others not included in his enumeration, or referred to, as far as I have been able to ascertain, in the works of other students of antarctic fungi; and it is the object of the present note to give some account of several of the latter, which were among the first that I met with in these fascinating woods.

On returning along the Rio de las Minas from my first excursion to the beech forest, I noticed on many of the smaller trees of *Nothofagus bicrenata* which covered the lower slopes of the ravine, especially on those which, from constant cropping by cattle, had assumed a bushy habit, but occasionally, also, on the lower

branches of larger trees, certain leaves, sometimes one or two together, but more often all the leaves of a twig or small branch, which were peculiar in appearance. These leaves were conspicuous from their paler yellowish-green color, which contrasted with the deep green of the healthy leaves, and were thicker and often distinctly larger than those of the normal foliage, as indicated in the accompanying text figure, photographed from dried material. Although every leaf of such twigs or branches was invariably affected, the latter showed little if any modification or distortion, and little if any tendency was observable to the formation of a witches broom, through the growth of adventitious shoots. The under side of these leaves were livid white in color, owing evidently to a continuous covering of asci, and I was greatly pleased to know that I had added a *Taphrina* to my overflowing basket of treasures.

On examining sections of this material, the asci proved to be rather stout, distally truncate or rounded, seated on a broader basal cell between the ruptured cutis and the epidermis, the outline of which was unbroken by any rhizoidal intrusion of the fungus between its cells. The asci were so densely filled with a very uniform coarsely granular fatty protoplasm, that no structures resembling spores were at first observed, and the material was laid aside on the assumption that it was immature. On reexamining it, however, and breaking the asci by crushing them, the coarse protoplasm was forced out, and I was astonished to see mingled with it great numbers of peculiar appendiculate bodies (fig. 6), so unlike any described ascospores of this group that it was not till I had actually seen them emerge from within the ascus when under pressure, that I was convinced of their true nature. After remaining in glycerin for some days, the granular contents of the ascus become modified, so that the spores, in different stages of development, are clearly visible (figs. 3, 4), and the origin of this singular habit in the mature spore is readily made out by a comparison of these stages (figs. 5, 6). The primary spores are always eight in number, relatively small in proportion to the size of the ascus (fig. 3), regularly oval in outline, and very uniform in size. As their development progresses, a bud appears at either extremity, which enlarges to form a stout, nearly cylindrical or somewhat

clavate, terminal appendage very constant in its form and dimensions, the axis of which coincides with that of the primary spore, and usually exceeds it in length. While these terminal appendages are developing, subterminal buds begin to appear about the base of each, normally four in number, less often two or three, which form a whorl of threadlike, divergent, slightly tapering appendages, rigid, straight or usually somewhat curved, and two to three times as long as the terminal ones. The origin of these subterminal

FIG. 1.—Branchlet of *Nothofagus antarctica* var. *bicrenata*, showing natural foliage at the left; the leaves at the right all attacked by the *Taphrina* and distinctly hypertrophied; slightly reduced from dried material.

appendages is often distinguished at maturity by a slight swelling, more or less clearly visible between the body of the primary spore and the base of the terminal appendage. As a result of the formation of these appendages, the primary spore is left nearly empty and is usually seen to be traversed by a single strand of protoplasm, while the terminal appendages, as they mature, become filled with dense refractive contents. These terminal appendages, moreover, evidently become the functional spores, since they readily separate from the empty primary spore, carrying with them the whorl of

threadlike subterminal appendages, which may perhaps be assumed to aid in their dissemination and lodgment after discharge. In crushed specimens these appendiculate terminal buds predominate, entire spores being comparatively infrequent.

That these extraordinary spores owe their peculiar structure at maturity to a specialization of the phenomenon which occurs in so many species of *Taphrina*, and which, through the budding of the primary spore, fills the ascus with yeastlike elements, seems highly probable; yet it is very remarkable that a phenomenon which, in other instances, is wholly indeterminate in character, the yeastlike elements being produced without regularity as to number, association, or differentiation as to function, should, in the present instance, be replaced by such a definite association of buds, which not only differ from one another in form and function, but are constant in number as far as the terminal buds are concerned, and at least subconstant as regards the subterminal ones. No further development nor any indication of germination in the primary buds was seen in any of the material examined.

The relation of the parasite to its host is a matter concerning which I have been unable to satisfy myself. In none of the sections examined, which were made from dried material, have I been able to detect any signs of fungus filaments penetrating the leaf or stem tissues, or extending themselves in any position except between the cutis and the epidermis. Nevertheless, the fact that all the adjacent leaves in branchlets of considerable size are completely involved, would point to the perennial nature of the disease, which may be presumed to extend from a hibernated mycelium in the young shoots to the unfolding leaves.

This species was subsequently found in abundance, not only along the ravine above mentioned, but on the larger trees of the forest, especially on the lower branches of such as grew along the margins of the open swampy glades characteristic of the region where I collected. It was also found less abundantly in the coastal region, not only on *Nothofagus antarctica* var. *bicrenata*, but also on the so-called var. *uliginosa*, a tree quite different in habit, leaves, and fruit, and growing in scattered colonies, especially to the south of the town of Punta Arenas. I may mention, in regard to these

hosts, that Professor SARGENT informs me that the determinations above given are confirmed by HEMSLEY, who suggests that the var. *uliginosa* should be considered a distinct species.

I saw no other species of *Taphrina* during my stay at Punta Arenas, nor did I find indigenous species elsewhere in Chile. About Santiago and in the central valley, where the Lombardy poplar is extensively planted, attaining a great size and forming one of the most conspicuous features of the landscape, the brilliant *T. aurea* was common, attacking the leaves of this host. *T. Ulmi* was also abundant on an introduced species of *Ulmus* planted about the Baños de Apoquindo, near Santiago; and throughout this whole region of the central valley the familiar *T. deformans* is destructive to the peach.

The *Taphrina* on *Nothofagus*, to which I have given a name suggested by the peculiarities of its spores, may be characterized as follows:

Taphrina entomospora, nov. sp.—Stratum ascorum livide-albidum, totam paginem inferiorem folii occupans, mycelio inter cuticulam et epidermidem nascente ortum: ascis dense confertis, subcylindricis, apice rotundatis vel subtruncatis, cellula basali latiore instructis; supra epidermidem positis: sporidiis entomomorphis, octonis, plasmate dense granuloso obscuratis; primum simplicibus, ovalibus; deinde appendiculatis, appendicibus biformibus; alteris utrinque terminalibus, rectis, cylindraceis vel subclavatis; alteris subterminalibus, saepissime quaternis, rigidis, tenuibus, divergentibus, subcurvatis, subattenuatis, utrinque cyclo oriundis: ascis 55—60×13—15 μ. Sporidiis 9—10×3—4 μ. Appendicibus terminalibus 8—12×3.5 μ, subterminalibus 15—25×0.8 μ.

In foliis vivis lutescentibus *Nothofagi antarcticae* var. *bicrenatae* et var. *uliginosae*. Punta Arenas, Magellanes, Chile.

My first day's foray yielded another remarkable fungus, associated with the *Taphrina* just described. While gathering material of the latter, I noticed that in some instances the leaves were covered by a glistening powder, and further examination showed that when the *Taphrina* occurred on twigs growing protected among the dense branches of small bushy trees, the powder was associated with reddish-brown perithecia evidently belonging to one of the Ery-

sipheae. This secondary parasite proved also not uncommon when sought for; but seldom fruited unless somewhat protected as above described. In one instance it was found spreading copiously from a twig affected by the *Taphrina* to the healthy foliage of the host; but in all other cases observed it was practically confined to leaves already affected by the other parasite. The perithecia being small and inconspicuous when scattered on the healthy leaves, it is not impossible that I may have overlooked it, and that it may naturally grow apart from the *Taphrina*. The reaction between the two, however, was very evident, the growth upon leaves invaded by the *Taphrina* being very much more luxuriant and the perithecia much more abundant. A similar phenomenon is seen in the case of the *Microsphaera* on *Berberis* referred to below, and may be comparable in a way to that seen in the Erysipheae inhabiting the hexenbesen of *Phytoptus* on *Celtis*, or the erinoses of *Fagus* and *Cephalanthus*. When examined microscopically, this fungus proved to be an *Uncinula* almost as peculiar as the *Taphrina* with which it was associated, owing to the very unusual modification of its appendages, which become distally twisted in a close spiral of striking appearance. The perithecia (fig. 7), which are usually epiphyllous, although sometimes amphigenous, are often densely crowded, of a reddish-brown color, globose-depressed, coarsely areolate. They show considerable variation in size (70–100 μ), and in the number of asci (5–8) contained in each. The appendages (figs. 7, 8) are 4–8 in number, without septa, the basal portion thick-walled and suffused with reddish brown, the suffusion involving also one or sometimes more than one turn of the spiral portion, which is otherwise quite hyaline and may show as many as eight turns, sometimes but half this number, ending in a helicoid extremity (figs. 8, 9), of characteristic contour, thin-walled, and somewhat inflated. The appendages are quite rigid, and curve somewhat upward from their insertion on the equatorial region, whence it is evident that the twisting does not assist in freeing them from the substratum, but, if it has any significance, must be supposed to enable them to become more readily attached to objects with which they may come in contact. A somewhat similar phenomenon is seen in *Sphaerotheca spiralis* Neger, discovered by DUSEN on *Escal-*

lonia rubra near the Lago Argentina in Patagonia, and very kindly communicated to me by Dr. NEGER. The spiral twisting of the appendages in this form, although distinct, is, however, more or less indefinite and decidedly irregular. A somewhat similar tendency is also seen in other species of *Uncinula*, and a variety on poplar of the common *U. salicis* has been distinguished as *U. heliciformis* by E. C. HOWE, owing to a similar though slight tendency to the production of a terminal spiral in the appendages. It seems certain, however, that no species of *Uncinula* hitherto described could be interpreted with sufficient liberality to include this antarctic form which may be characterized as follows:

Uncinula Nothofagi, nov. sp.—Epiphyllus vel rarius amphigenus: peritheciis mycelio albido persistenti effuso insedentibus, dense congestis vel discretis, globoso-depressis, 80 μ diam. (70–100 μ), rufo-brunneis, cellulis 10–20 μ diam.: appendicibus 5–15, aseptatis, 70–100 μ longis, inferne rectis vel curvatis, rigidis, induratis, brunneo-suffusis; superne spiraliter arcte 4–8 convolutis, apice helicoideo-subinflatis, spiris basalibus plus minus suffusis, ceteris hyalinis: ascis late ovalibus, 5–8 in quoque perithecio, suboctosporis; sporidiis oblongo-ellipsoidiis 18–20×10 μ: conidiis subcylindraceis, 25–32×10–15 μ.

In foliis *Nothofagi antarcticae* var. *bicrenatae*, *Taphrina* occupatis vel rarius eis in folia sana migrans. Punta Arenas, Magellanes, Chile.

Much to my surprise, the *Uncinula* above described proved to be not the only species having this peculiar habitat, and among the small shrubby trees of *N. bicrenata* which grow to the south of the town in the califate pastures, I several times encountered a very different species, always on leaves attacked by the *Taphrina*. This form was decidedly rare and only a small amount of material was obtained by diligent searching. The two species were easily distinguished with a hand lens, the large perithecia of the second form being sparingly produced, its long irregularly flexed appendages, which in many perithecia are undeveloped, lacking the spiral coils of its ally and ending in an open hook, or half-helix, more or less characteristic in contour, and recalling the tip of a golf stick or the curved handle of an umbrella (fig. 12). In general these appendages are decidedly more than twice as long as the

diameter of the perithecium (fig. 11), quite hyaline, their outline somewhat uneven with an occasional slight irregular swelling. The perithecia which almost always occur on the upper side of the leaf, as far as I have seen, are much larger than those of *U. Nothofagi*, and contain many more (10–20) asci, each with three or four spores instead of eight. Since it does not seem possible to refer this form to any of the described species of *Uncinula* it may be characterized as follows:

Uncinula magellanica, nov. sp.—Plerumque ephiphyllus. Peritheciis mycelio albido effuso exiguo insidentibus, discretis vel subgregariis, globoso-depressis, opacis vel subopacis, atro-brunneis, 130 μ (90–150 μ) diam., cellulis 10–20 μ latis; appendicibus 10–22, hyalinis, longis, tenuibus, curvatis vel subflexuosis, subrigidis, 225–400×5–6 μ, apice subinflatis et subrecurvatis: ascis late clavatis, 55×25 μ, plerumque 3–4 sporis, sporidiis 20×10–12 μ: conidiis subcylindraceis, 35–40×15–18 μ.

In foliis *Nothofagi antarcticae* var. *bicrenatae*, *Taphrina* obsessis. Punta Arenas, Magellanes, Chile.

Three other species of Erysipheae were also found in the neighborhood of Punta Arenas. Of these a form, encountered but once on a species of *Galium*, appears to be *Erysiphe Chicoracearum;* while another not uncommon on several Compositae does not seem to differ from *Sphaerotheca fuliginea*. The third, however, is quite remarkable on account of its habitat; since, like the two species of *Uncinula* just described, it appears to be invariably associated with another fungus. Toward the end of February I noticed that the distortions on *Berberis buxifolia* caused by *Aecidium magellanicum* were assuming a whitish appearance from the invasion of an *Oidium* that covered the leaves and twigs which were attacked by the rust; and early in March it was almost impossible to find a specimen that was not more or less completely covered by it. I looked in vain for perithecia, however, and it was not until the very last days of my stay (March 10) that I was able to obtain a rather scanty supply of leaves bearing scattered perithecia, many of which were fully matured. The latter proved to belong to a species of *Microsphaera* which I am unable to distinguish from *M.*

Alni. Indeed it appears to be closer to the typical form of this species than most of the varieties of the latter. The habitat, however, is certainly remarkable; and although I made a special effort to find even the *Oidium* apart from the *Aecidium*, I never succeeded in doing so.

I find but one other species of this family recorded from Punta Arenas, in fact the only other species, I believe, which has been hitherto recorded from this locality. This was found by SPEGAZZINI on *Ribes magellanicum* and is mentioned in his *Fungi Patagonici* (p. 34). It was also found by him on the same host in Tierra del Fuego and described as *Phyllactinia antarctica* Speg., a name which is not recognized in SALMON'S *Monograph*, where it is placed as a synonym of *P. Corylea*. Although *Ribes magellanicum* was not uncommon along the ravine of the Rio de las Minas, I did not discover this *Phyllactinia*, not being aware at the time that it should be sought for on this host.

HARVARD UNIVERSITY

EXPLANATION OF PLATES XVIII AND XIX

The figures were drawn with camera lucida from preparations, in glycerin, of sections cut from dried material, and are reduced about one-fourth. The following combinations of objectives and oculars were used in making the drawings: figs. 1, 2, Zeiss D, oc. 4; figs. 3–6, Leitz water immers. 10, oc. 4; fig. 7, Leitz C, oc. 4; figs. 8–10 and 12, 13, Leitz water immers., oc. 1; fig. 11, Zeiss A, oc. 4.

PLATE XVIII

Taphrina entomospora Thaxter

FIG. 1.—Portion of the lower surface of a leaf showing the ascus primordia lying between the cutis and the epidermis; one at the right beginning to develop.

FIG. 2.—Portion of section showing asci.

FIG. 3.—A single ascus containing eight ascospores which have not yet begun to bud.

FIG. 4.—A more mature ascus in which the spores have developed their characteristic appendages.

FIG. 5.—Three ascospores in which the appendages are in process of formation.

FIG. 6.—Six mature or nearly mature spores with their appendages.

PLATE XIX

Uncinula Nothofagi Thaxter

FIG. 7.—Two perithecia showing variably developed appendages, the upper shown in surface view, the lower showing the appearance of the eight asci seen partly in optical section.

FIG. 8.—A single well developed appendage enlarged.

FIG. 9.—The tips of two appendages enlarged.

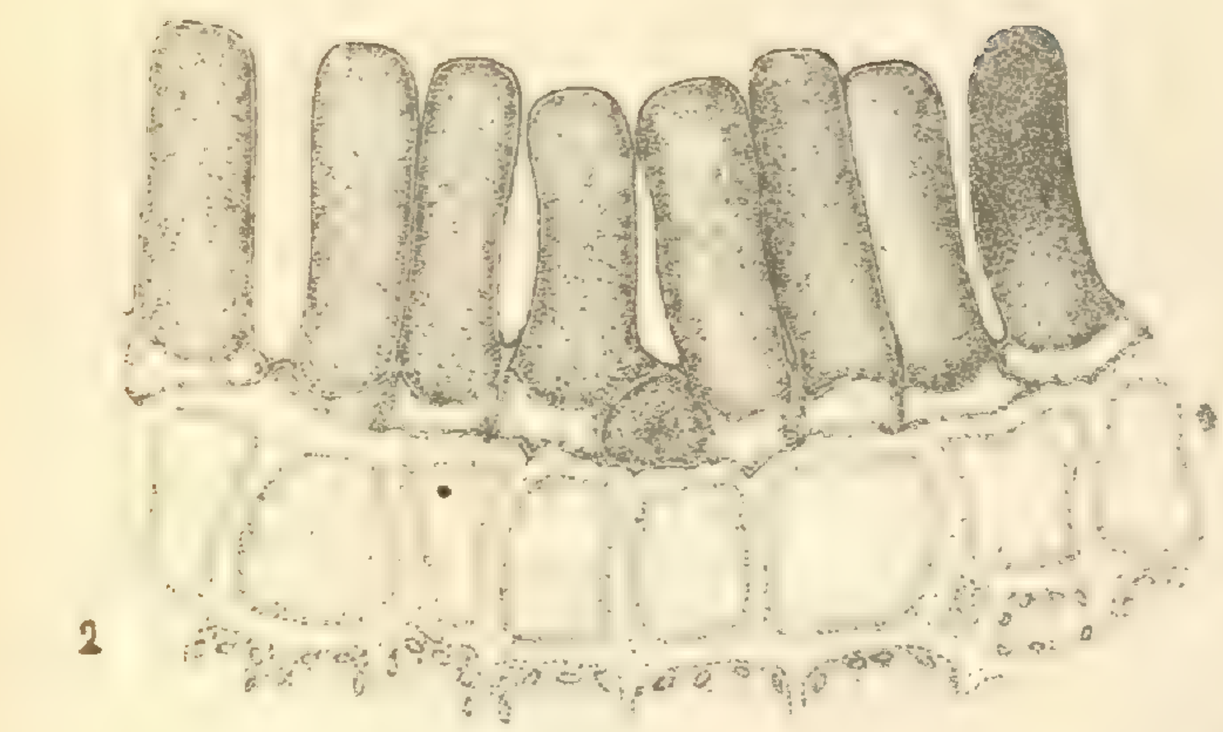
FIG. 10.—Two asci.

Uncinula magellanica Thaxter

FIG. 11.—A single perithecium.

FIG. 12.—A single appendage and three tips of appendages enlarged, showing variations in the terminal hooks.

FIG. 13.—Two asci.



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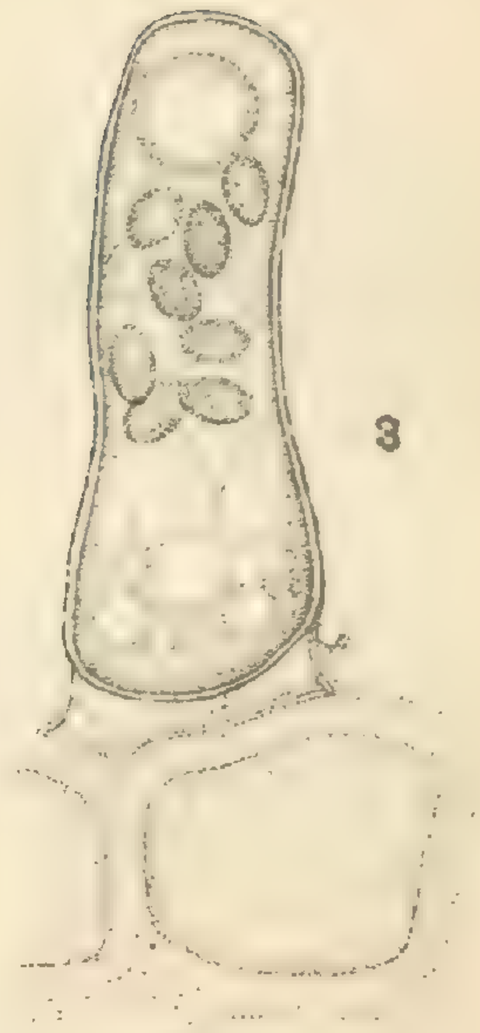

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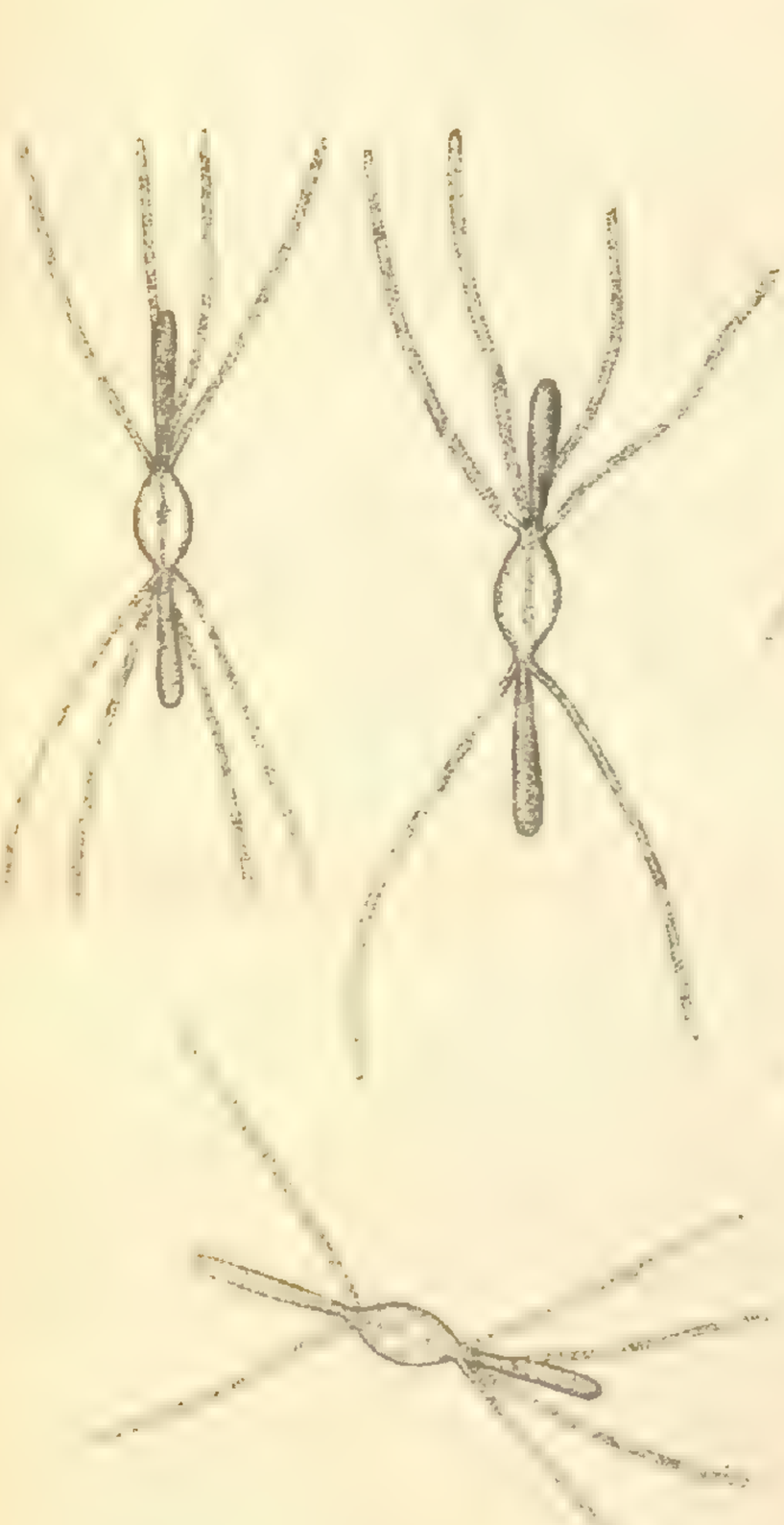

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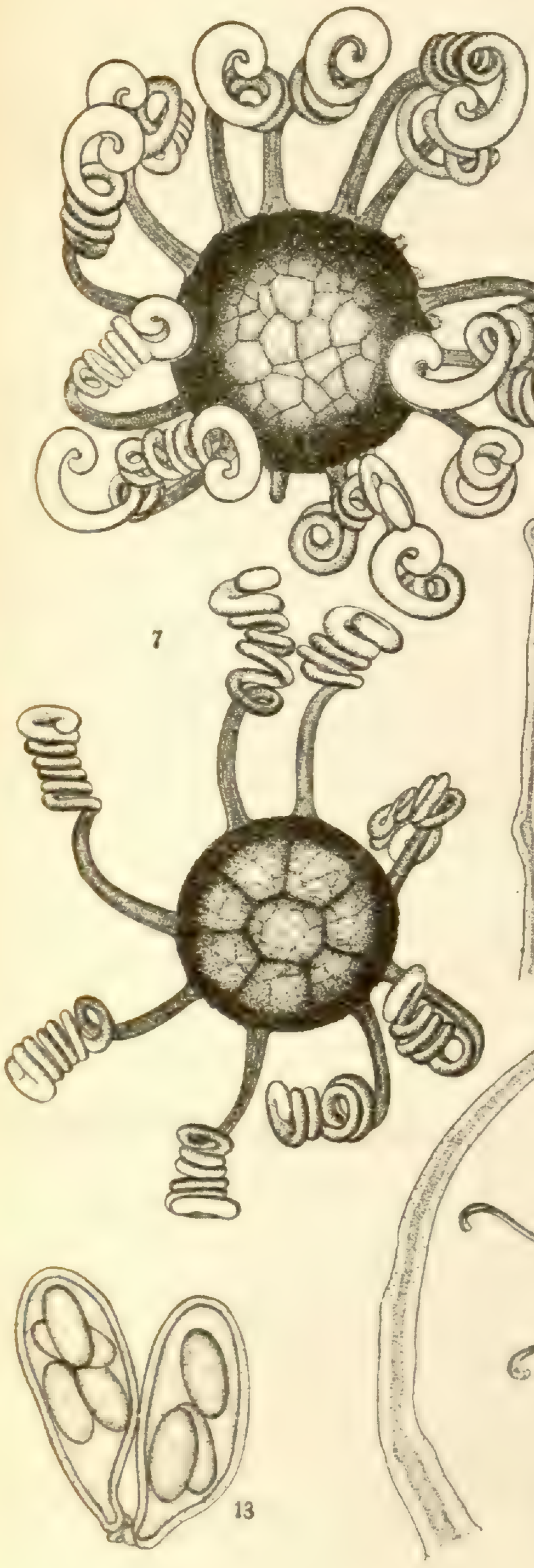
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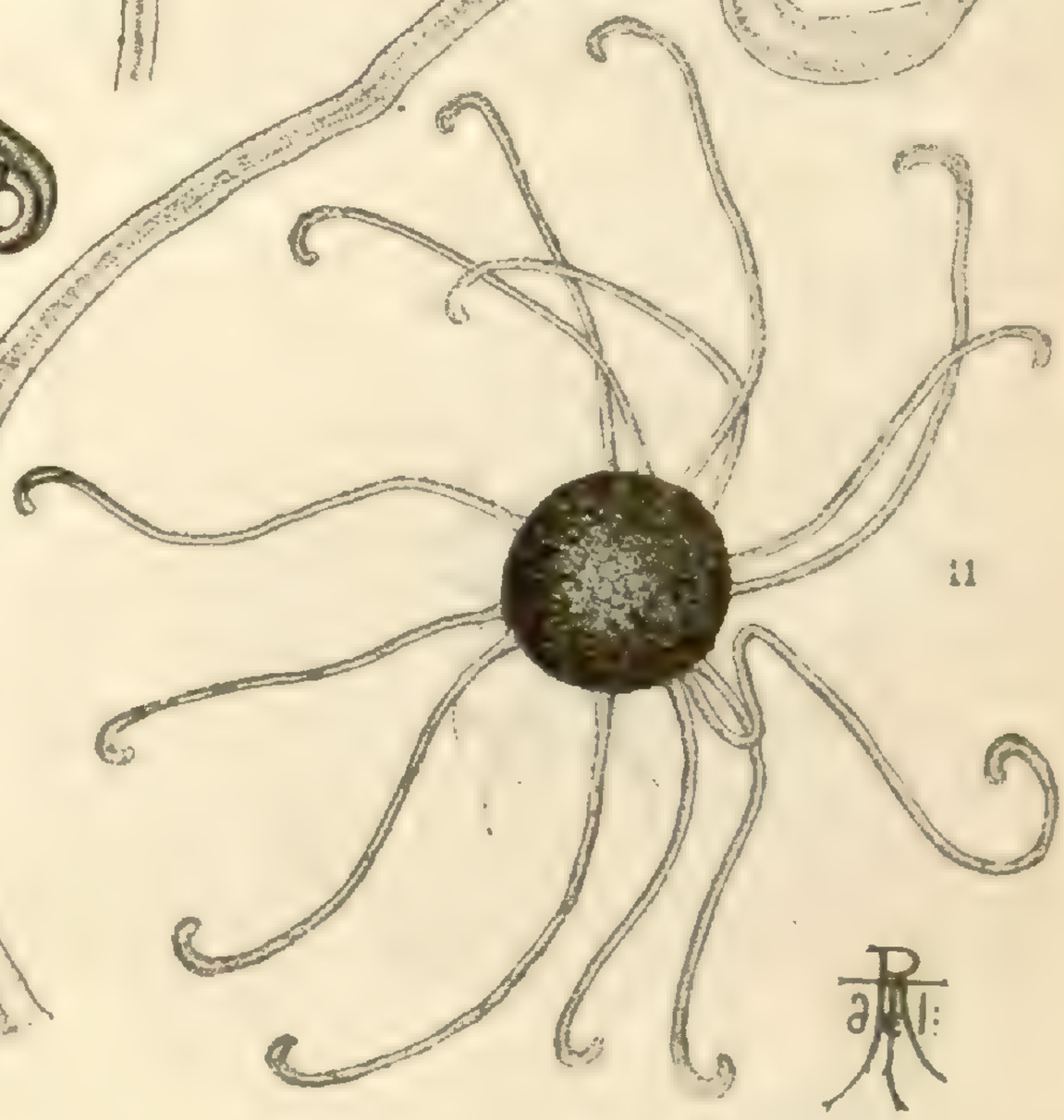
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THE DEVELOPMENT OF THE ASCOCARP OF LEOTIA[1]

WILLIAM H. BROWN

(WITH FORTY-SEVEN FIGURES)

The present study is based upon material of *Leotia lubrica* and *L. chlorocephala* collected at Cold Spring Harbor, Long Island. For microscopical study, sections were cut 2 and 3 μ thick and stained with either Haidenhain's iron-alum hematoxylin or Flemming's triple stain.

Leotia lubrica

Leotia lubrica grows in damp places among various species of mosses. Several ascocarps are often connected together by their bases, and sometimes a small one may grow out from the base of a mature specimen.

The age of an ascocarp cannot always be told from its size, for one 3 mm. long may be more mature than one about 1 cm. in length. The youngest specimens found were about 1.5 mm. long, and were nearly conical in shape (fig. 1). When the ascocarp has reached a length of about 2 mm., the tip of the cone begins to enlarge to form the head (figs. 2, 3); this is about the stage at which the hymenium begins to be differentiated. The ascocarp soon assumes the mature form (fig. 4), and the further changes are largely those of growth. The hymenium now covers the upper surface and margin of the head. The upper surface may continue to grow until its margin becomes curved in toward the stalk (fig. 5).

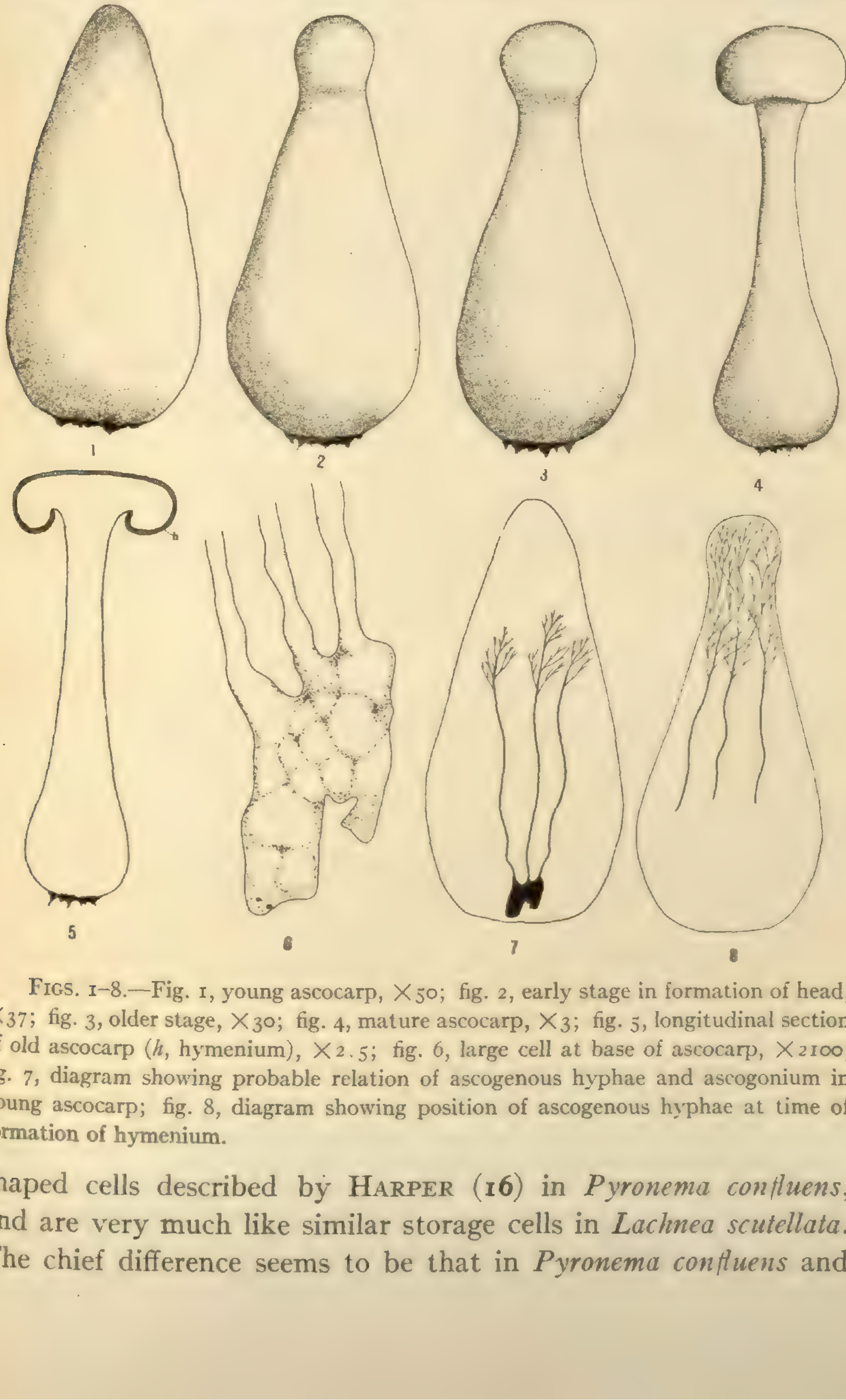
The youngest specimen found was composed largely of densely interlacing vegetative hyphae. At the base of the ascocarp there was a very large cell (fig. 6) from which a number of large hyphae extended upward toward the tip of the ascocarp. This large cell was vacuolated and its contents had degenerated, giving it all the appearances of an emptied ascogonium. The hyphae arising from this cell were empty, as is usually the case in old ascogenous hyphae, and so could not be traced with certainty for any great distance.

[1] Contribution from the Botanical Laboratory of the Johns Hopkins University, no. 17.

They appear, however, to be connected with similar hyphae which become very distinct only a little farther up (about 10 μ) in the ascocarp. These latter hyphae, of which there are three or four, are the ascogenous hyphae. They are very much larger than the surrounding vegetative hyphae, and in the character of their contents are quite distinct from them. The ascogenous hyphae become more and more distinct as they get nearer the tip of the ascocarp, but they show little tendency to branch until they have reached about one-half the distance from the base to the tip, when they divide to form a large number of smaller, much branching hyphae. These latter hyphae have a tendency to spread out as well as to grow upward, but in young specimens they are of course near the larger hyphae. Assuming that the large cell at the base of the ascocarp is an ascogonium, as seems to be the case, and that it is connected with the ascogenous hyphae, this stage may be represented diagrammatically as in fig. 7, in which the black lines represent the ascogenous hyphae. In slightly older specimens the ascogenous hyphae have spread over the entire tip. At about this time the tip enlarges to form the head of the ascocarp. Some of the vegetative hyphae soon grow out to form the paraphyses, after which the ascogenous hyphae give rise to asci. This stage is represented diagrammatically in fig. 8, in which the black lines still represent the ascogenous hyphae, the older parts of which have disappeared.

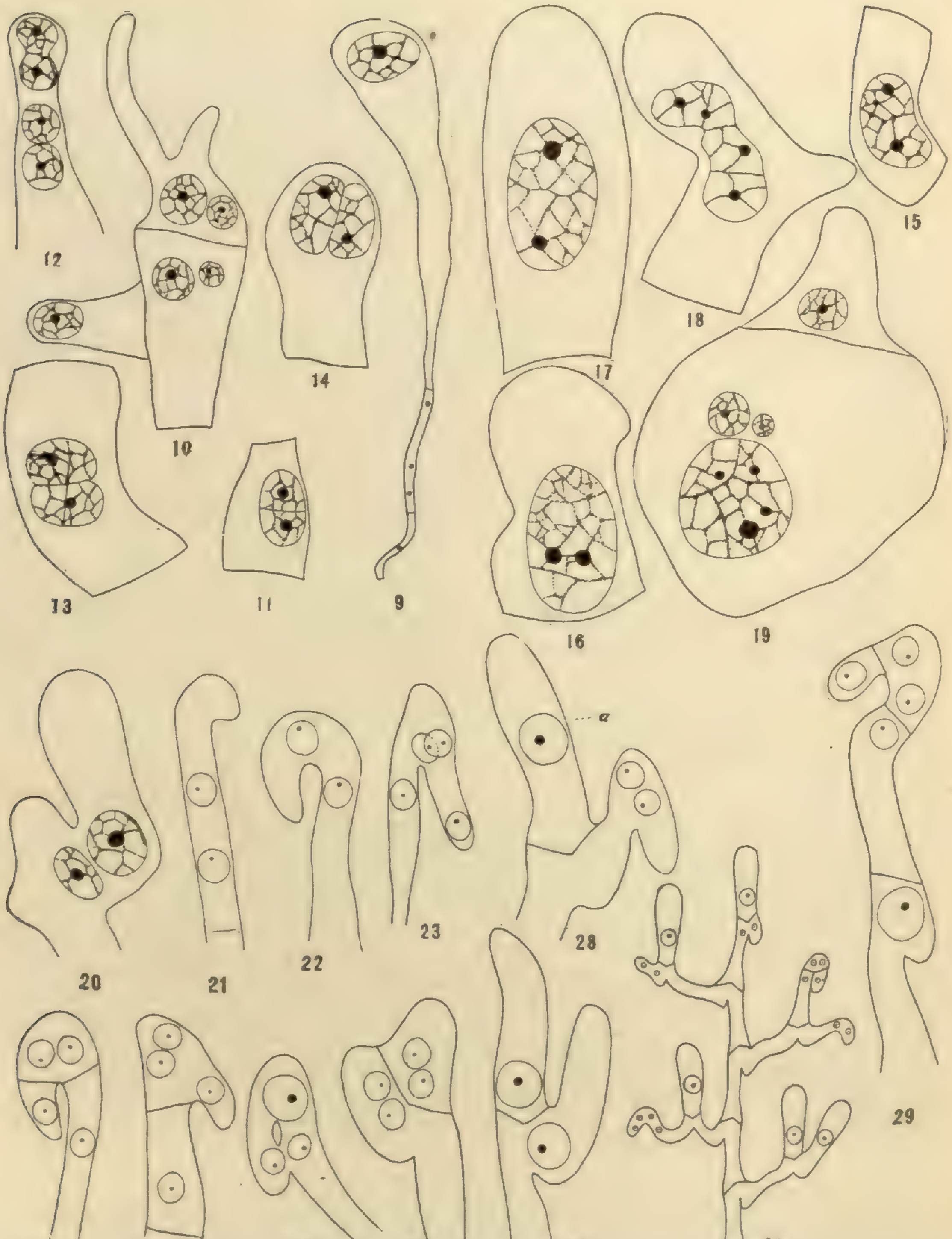
While the hymenium is being differentiated, some of the vegetative hyphae give rise to large storage cells (fig. 9). This process is similar in the two species studied and the same description will apply to both. These large storage cells are formed in rows and give rise to paraphyses (fig. 10). The storage cells are at first multinucleate, but the nuclei usually fuse as growth proceeds (figs. 11–14). This process continues until often the cells contain a single, very large nucleus, many times the size of the largest nucleus in the ascus (figs. 15–17). Frequently the nuclei are very irregular (fig. 18). In other cases, a cell may contain a very large nucleus with several much smaller ones lying near it (fig. 19). These last two cases suggest amitoses, but may very well be stages in fusion. The storage cells may have a very irregular shape

(fig. 20), or they may be quite regular (fig. 17). They are relatively much more abundant in young ascocarps than in the older ones. The storage cells seem to have the same function as the barrel-



FIGS. 1–8.—Fig. 1, young ascocarp, ×50; fig. 2, early stage in formation of head, ×37; fig. 3, older stage, ×30; fig. 4, mature ascocarp, ×3; fig. 5, longitudinal section of old ascocarp (*h*, hymenium), ×2.5; fig. 6, large cell at base of ascocarp, ×2100; fig. 7, diagram showing probable relation of ascogenous hyphae and ascogonium in young ascocarp; fig. 8, diagram showing position of ascogenous hyphae at time of formation of hymenium.

shaped cells described by HARPER (16) in *Pyronema confluens*, and are very much like similar storage cells in *Lachnea scutellata*. The chief difference seems to be that in *Pyronema confluens* and



FIGS. 9–31.—Fig. 9, vegetative hyphae giving rise to storage cell; fig. 10, paraphyses growing out from storage cells; figs. 11–14, fusion of nuclei in storage cell; figs. 15, 16, nucleus with two nucleoli in storage cell; fig. 17, large storage cell with single very large nucleus; fig. 18, storage cell with very irregularly shaped nucleus; fig. 19, storage cell containing one large and two small nuclei; fig. 20, an irregularly shaped storage cell; figs. 21, 22, tip of ascogenous hypha with two nuclei; fig. 23, two nuclei in tip of hypha have divided to four; fig. 24, walls have come in, separating sister nuclei; fig. 25, hook in which there is no wall cutting off uninucleate ultimate

Lachnea scutellata the nuclei of the storage cells probably do not usually fuse.

The details in the formation of the asci were studied chiefly in *Leotia chlorocephala*, and will be described in connection with that species. The appearance of the hymenium suggests, however, that the process is similar in the two cases.

Leotia chlorocephala

The ascogenous hyphae in *Leotia chlorocephala*, as in *L. lubrica*, have their origin in the stipe. The hymenium is also formed in the same way that has been described for *L. lubrica*.

In 1894 DANGEARD described the asci of *Peziza vesiculosa* as originating from a binucleate penultimate cell of an ascogenous hypha. Since that time the same phenomenon has been described by various workers in a number of forms. A large number of these are mentioned by OVERTON (23). The usual case seems to be that there are two nuclei in the tip of an ascogenous hypha. These divide simultaneously and walls come in between the sister nuclei of the two pairs, thus forming a binucleate penultimate cell and a uninucleate ultimate and antepenultimate cell. The ascus is then formed from the binucleate penultimate cell. MAIRE (20) and GUILLIERMOND (14) have described the asci of *Galactinia succosa* as originating from a binucleate ultimate cell. In *Humaria granulata* (BLACKMAN and FRASER 4) the asci usually arise from a binucleate penultimate cell, but in two cases the asci had a terminal position.

In speaking of *L. chlorocephala* and a number of other ascomycetes, FAULL (11) says: "It is quite probable that the only

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cell; fig. 26, hook in which two nuclei have fused to form nucleus of ascus, and tip has fused with stalk of hook; fig. 27, ultimate cell has fused with antepenultimate; nucleus of latter has migrated into former, which is growing out to give rise to ascus or another hook; fig. 28, two nuclei of penultimate cell have fused to form nucleus of ascus; ultimate cell has fused with antepenultimate, and nucleus of latter has migrated into former, which has grown out to form another hook; fig. 29, binucleate penultimate cell has given rise to hook; ultimate cell has fused with penultimate, and the two nuclei have fused; ultimate cell has not developed further; fig. 30, binucleate penultimate cell has formed ascus, which fusion product of ultimate and antepenultimate has given rise to second ascus; fig. 31, diagram illustrating multiplication of number of asci by method shown in figs. 26–30; figs. 9–20, ×1400; figs. 21–30, ×2100.

departure from the type is the lack of the cross wall that cuts off a uninucleate cell at the tip of the hypha." Later on he says that in some of the species the cross wall may be exceptionally present. In this statement he probably includes *L. chlorocephala*, as the cross wall is frequently present in this species. *L. chlorocephala*, however, shows quite a number of other deviations from what has been regarded as the usual type.

The tips of the ascogenous hyphae in the hymenium usually contain two nuclei, and become shaped like a hook (figs. 21, 22). The nuclei then divide, giving rise to four nuclei (fig. 23). Walls may then come in between the sister nuclei (fig. 24), or the wall cutting off the terminal cell may not be developed (fig. 25), or in still other cases both walls may be lacking even after the two nuclei in the bent portion of the hook have fused to form the nucleus of an ascus (fig. 26). When the nuclei are distributed as in figs. 23, 24, so that one is in the tip and two in the bent part of the hook, the two nuclei (apparently not sisters) in the bent portion may fuse to form the nucleus of an ascus (figs. 26, 28*a*), or they may give rise to the four nuclei of another hook (fig. 29). The uninucleate tip usually grows down and fuses with the stalk of the hook (fig. 26). The nucleus of the stalk may then migrate out into the tip (fig. 27), which usually grows out to form another hook (fig. 28), or sometimes an ascus (fig. 30). That in these cases it is the tip which has developed below the ascus is shown by the presence of the curved end of the tip joined to the stalk cell, as well as by the presence of both the wall which separated the ultimate cell from the penultimate and the one which divided the penultimate from the antepenultimate. The nucleus from the tip of a hook may occasionally migrate into the stalk. Sometimes the nucleus formed by the fusion of the nuclei of the tip and stalk does not develop further (fig. 29). This is usually associated with a vacuolated condition of the cytoplasm which indicates that the failure of the tip to develop is due to a lack of food. The processes described above, by which either the tip or bent portion of a hook may form another hook, are apparently often repeated many times, so that even in a young stage of the hymenium five or six hooks are frequently seen joined together in various ways. This is shown diagrammatically in fig. 31.

This same method of multiplication of asci occurs in *Geoglossum* sp. (figs. 32–38). The two nuclei in the tip divide to four (fig. 32) and walls come in between the nuclei of each pair of sisters (fig. 33). The antepenultimate cell may then form an ascus (figs. 37, 38) or another hook (figs. 35, 36). The ultimate cell usually fuses wlth the stalk (figs. 34, 35). The nucleus of the ultimate cell may then migrate into the antepenultimate (fig. 35), but usually the nucleus of the antepenultimate cell migrates into the ultimate (fig. 34), which then grows out (fig. 36) to form a hook (figs. 37, 38) or an ascus.

The phenomena connected with the formation of the asci as just described in *Leotia* and *Geoglossum* have been observed by the writer in *Lachnea scutellata*, as reported before the Botanical Society of America at the 1909 meeting (**6**). In a paper read at the same time before Section G of the A.A.A.S., McCubbin (**21**) described the penultimate cell of the ascogenous hyphae of *Helvella elastica* as forming either an ascus or a hook. The ultimate cell frequently fuses with the antepenultimate, after which the nucleus of the antepenultimate migrates into the ultimate. The two nuclei then migrate into a process which grows out from the ultimate to form another hook. In *Humaria rutilans* Miss Fraser (**12**) has described the uninucleate ultimate cells of the ascogenous hook as growing out to form other asci. She says that where such proliferation had taken place the tip was usually connected with the stalk, and in one case the nucleus of the tip was migrating into the stalk. She did not determine, however, whether or not the nucleus of the stalk took part in the formation of new asci. It seems probable, however, that she has observed something of the same phenomenon that has been described in *Leotia*. The writer (**5**) has described the ultimate cell of *Pyronema confluens* as growing out to form other asci. In such cases a nucleus could not be found in the stalk cell, and so it may be that it had migrated into the ultimate cell and had then taken part in the formation of the hook. The presence of these phenomena in such rather distantly related species as those mentioned above suggests that they may be of rather frequent occurrence.

Remembering that the nuclei in the binucleate antepenulti-

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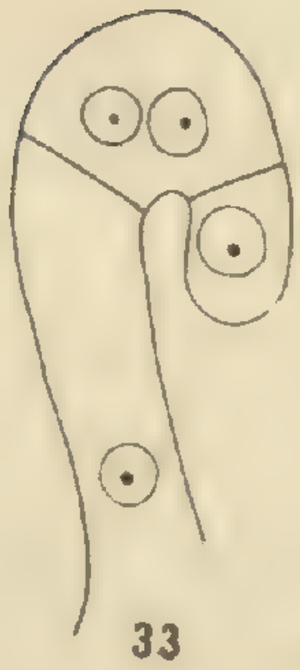
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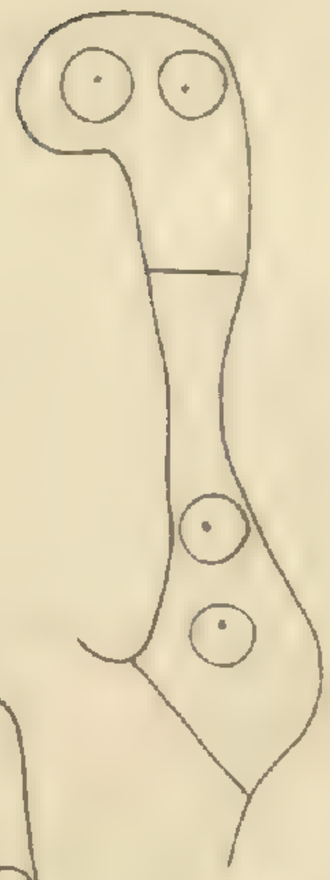
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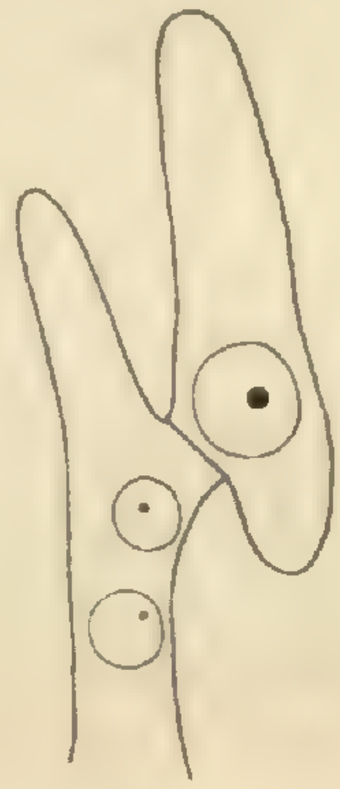
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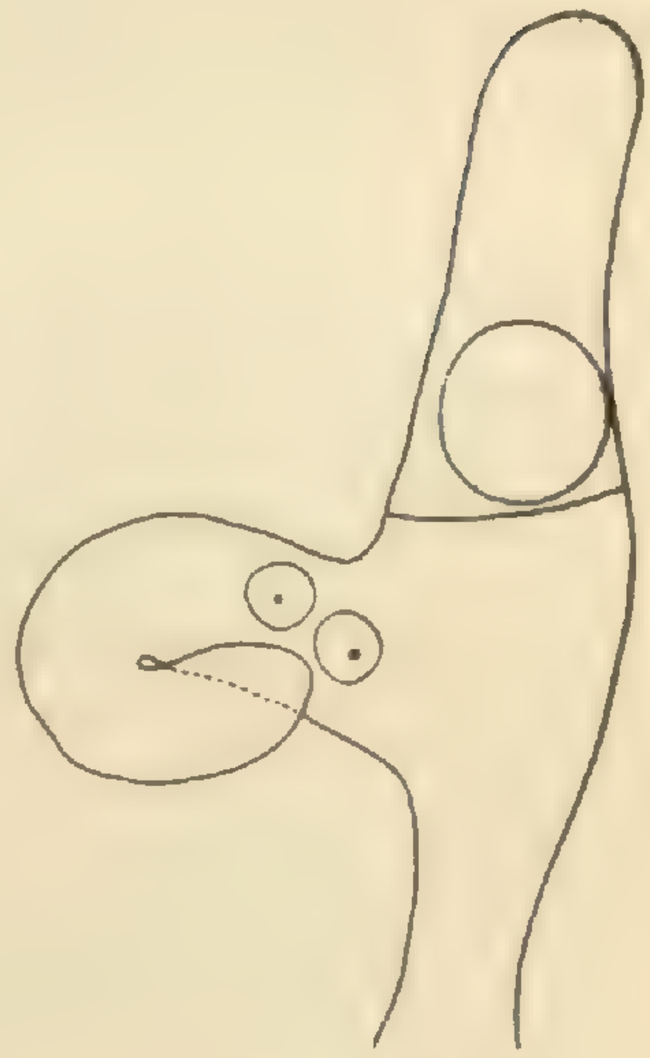
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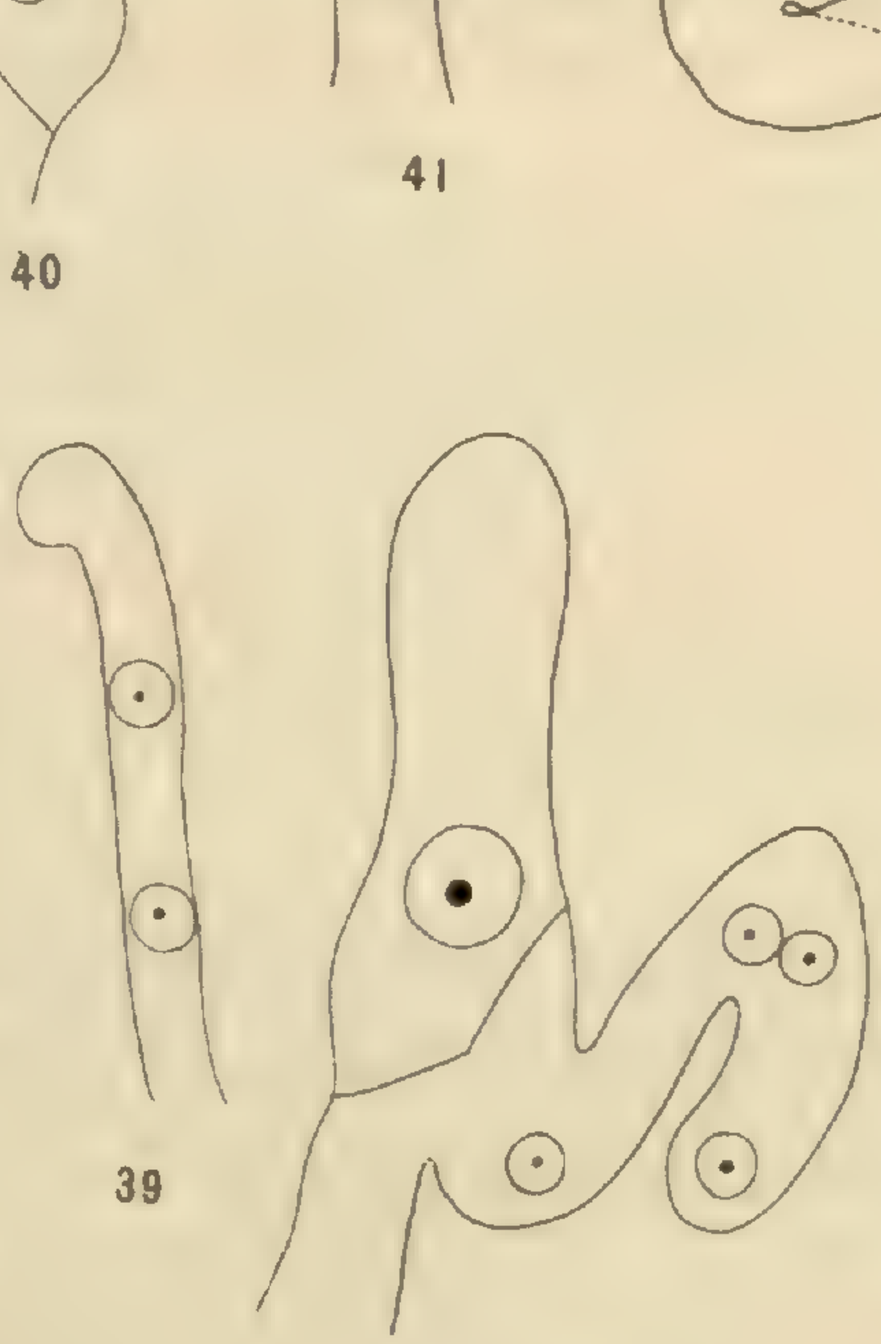
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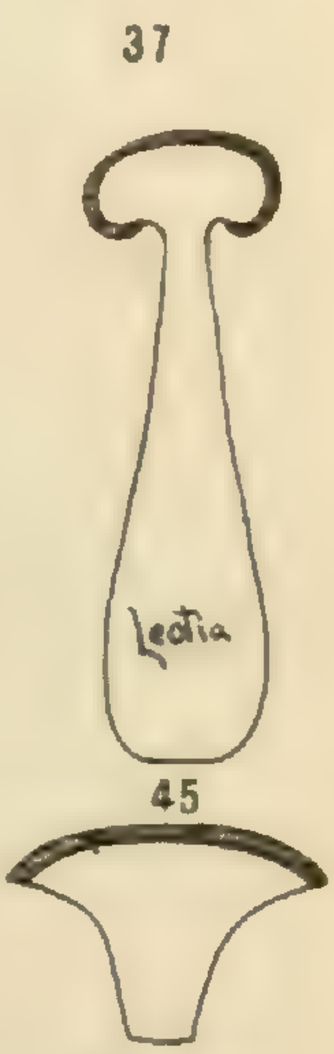
Pyronema
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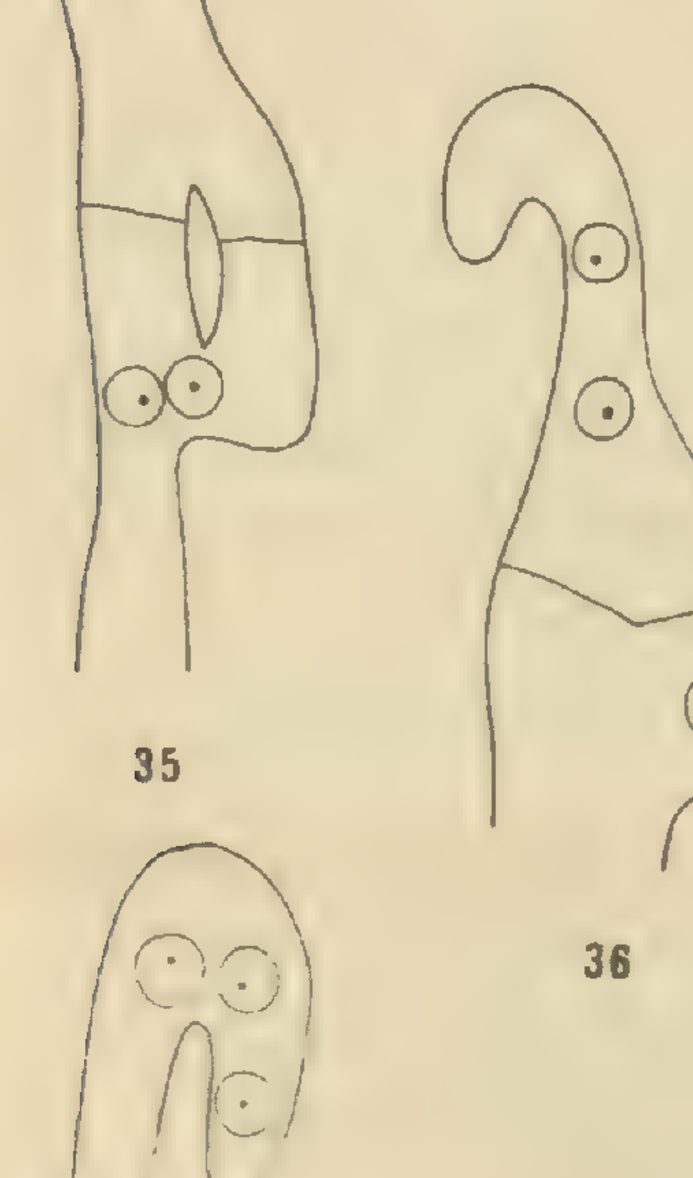
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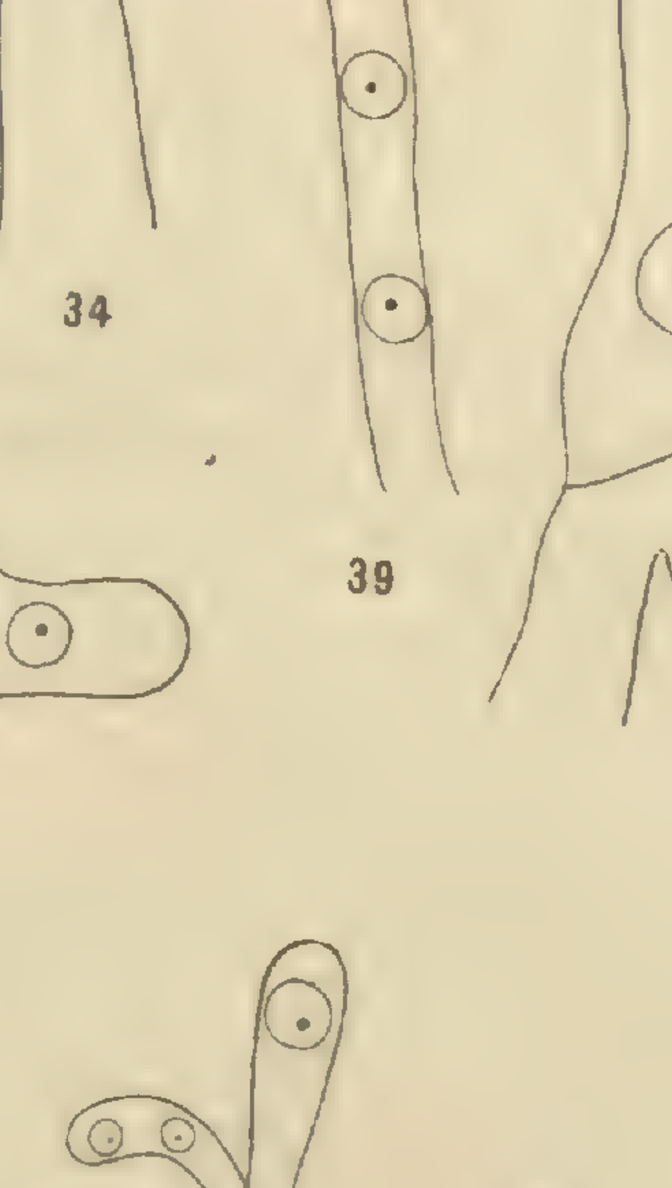
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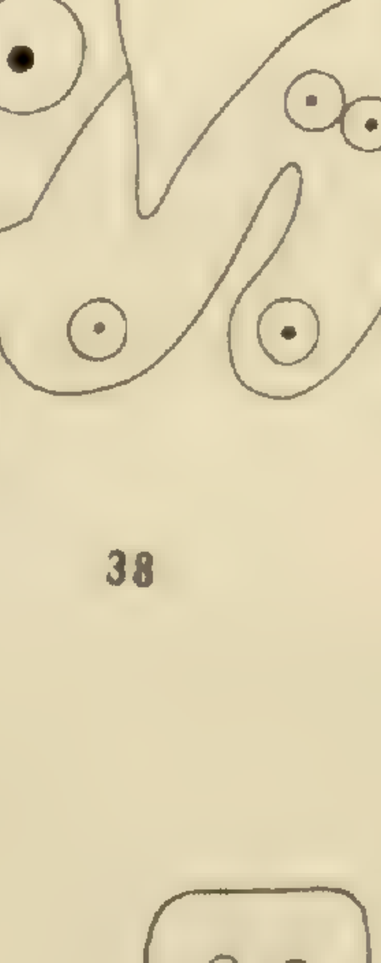
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mate cell are not sisters, but are composed of one nucleus from each of two pairs of sisters, it will be seen that every time either the ultimate or penultimate cell, if formed in the manner described above, gives rise to a hook, the distance of the relationship of the nuclei which fuse to form the nucleus of the ascus is increased. This can hardly be of any significance, however, in the case of *L. chlorocephala*, for, as will be shown later, two nuclei which are apparently sisters often fuse to form the nucleus of an ascus. It seems probable, therefore, that in *Leotia* the only use of the continued growth of the ultimate and penultimate cells is to increase greatly the number of asci which can be formed from a single hypha.

In *L. chlorocephala* the asci are also formed by another method, which probably occurs about as frequently as the one already described. In this case the tip of the hypha does not bend as much as in the first (fig. 39). When the nuclei have divided, a wall comes in between the two pairs of sister nuclei (fig. 40). That the two nuclei in each cell are sisters would seem to be shown by the fact that the hyphae appear to be too narrow to allow a side-by-side division of the nuclei, or for the nuclei to migrate past each other. There is, moreover, no evidence that such a parallel division or migration of the nuclei does occur. The two nuclei of the ultimate cell may fuse to form the nucleus of an ascus (fig. 41), or they may give rise to the four nuclei of another hook (fig. 42). That the asci and hooks in these cases are formed from a binucleate terminal cell is shown by the presence of the tip of the

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mate has grown out; figs. 37, 38, binucleate penultimate cell has formed ascus, while ultimate with nucleus from antepenultimate has given rise to hook; fig. 39, tip of ascogenous hypha with two nuclei; fig. 40, the two nuclei have divided to four and a wall has separated the two pairs of sister nuclei; fig. 41, two nuclei of ultimate cell have fused to form nucleus of ascus; penultimate cell is growing out to give rise to hook or ascus; fig. 42, both ultimate and penultimate cells have formed hooks; fig. 43, penultimate cell (*a*) has not developed further, while ultimate has given rise to hook similar to that shown in fig. 24; binucleate penultimate cell of this hook has formed ascus, while ultimate and antepenultimate have given rise to still another hook; fig. 44, diagram illustrating multiplication of asci by method shown in figs. 39–43; fig. 45, diagram of structure of ascocarp of *Leotia;* fig. 46, diagram of structure of ascocarp of *Pyronema omphaloides;* fig. 47, diagrammatic comparison of conjugate divisions in *Leotia* and in the rusts; figs. 32–43, ×2100.

hook at their bases. The binucleate penultimate cell may also grow out (fig. 41) to form a hook (fig. 42), or sometimes an ascus. In other cases it does not develop further (fig. 43). When this occurs the two nuclei may or may not fuse. Fig. 43 shows a case in which two binucleate cells were formed, the terminal one of which developed into a three-celled hook of the type first described. This hook then gave rise to an ascus and a second hook. It is clear from this that the same hypha may behave differently at different times. The formation of two binucleate cells may be repeated several times, as is shown diagrammatically in fig. 44.

In *Verpa bohemica*, FAULL (11) found the asci connected with the first, second, third, or fourth cell from the tip, but did not determine whether the asci grew out from the third or fourth cell, or whether the terminal cell underwent division after the budding out of the ascus.

In *Anixia spadicea* and *Urnula craterium*, FAULL (11) says that it looks as if the ascus might spring from any cell whatever. Judging from FAULL'S figures, all of the above cases might perhaps be explained as due to the two methods of multiplication of asci described in *Leotia*.

In *L. chlorocephala* the ascus soon after its formation grows out into a much elongated cell. Its nucleus divides three times, in the manner usual among the nearly related Pezizineae, and gives rise to the nuclei of the eight spores. The spores are at first round, but by subsequent growth they become elongated and vacuolated.

Systematic position of Leotia

ENGLER (10) places *Leotia* in a group near the Pezizineae. The observations recorded above seem to confirm this view of the near relationship. The large cell, probably an ascogonium, at the base of the ascocarp and the presence of the ascogenous hyphae in the stipe suggest a homology with those Pezizineae in which the asci are formed from a single ascogonium, as *Lachnea scutellata*, *Peziza granulosa*, *Ascobolus pulcherrimus* (WORONIN 29), *Ascobolus furfuraceus* (JANCZEWSKI 17, HARPER 15, WELSFORD 28), *Ascodemus nigricans* (VAN TIEGHEM 27), *Ryparobius* sp. (BARKER 1),

Thelebolus stercoreus (RAMLOW 24), *Humaria granulata* (BLACKMAN and FRASER 4), *Lachnea stercorea* (FRASER 13), and *Ascophanus carneus* (CUTTING 7).

As has already been pointed out, the origin of the hymenium, including the storage cells and the formation of the asci, is also similar to the same process in some of the Pezizineae.

The presence of an elongated stipe, moreover, is of frequent occurrence among the Pezizineae, while a tendency of the hymenium to become recurved is shown by many of them. A comparison of figs. 45 and 46 will show the similarity in form between *Leotia* and an old specimen of *Pyronema confluens*.

From the above considerations it would seem that *Leotia* is as closely related to some of the Pezizineae as some of them are to each other, and it is probable that the ancestors of *Leotia* were closely similar to some of them.

Relationship of the fusing nuclei

According to what is probably the most prevalent interpretation, the fusion in the ascus is regarded as being of a vegetative character, and so the relationship of the fusing nuclei is considered to be of no great significance. This interpretation is based on the presence of a supposed fusion of nuclei in the ascogonium. Such fusions have been described in *Pyronema confluens* (HARPER 16), *Humaria granulata* (BLACKMAN and FRASER 4), *Lachnea stercorea* (FRASER 13), *Ascobolus furfuraceus* (WELSFORD 28), *Humaria rutilans* (FRASER 12), and *Ascophanus carneus* (CUTTING 7). CLAUSSEN (8), however, after a study of *Pyronema confluens*, has come to the conclusion that the fusion in the ascus is the only one that occurs in that species. BROWN (5) has described a form of *Pyronema confluens* in which the antheridium does not fuse with the ascogonium, and in this case he fails to find a fusion of nuclei in the ascogonium. The cytology of the ascus confirms this interpretation. There are, however, appearances in this form very much like fusing nuclei, which are due, however, to the fact that the daughter nuclei reorganize close together. BARKER, in studying *Monascus*, failed to find a fusion of nuclei in the ascogonium, but attributed this to his failure to get the proper stages. SCHIKORRA

(25) describes the fusion of the antheridium and ascogonium in *Monascus*, but does not find any fusion of nuclei except in the ascus. In *Lachnea scutellata* the writer has been unable to find any fusion of nuclei except the one in the ascus. The haploid number of chromosomes persists throughout the vegetative hyphae, ascogonium, and ascogenous hyphae; while the diploid number exists only in the primary nucleus of the ascus. There are, however, appearances in the ascogonium and other parts of the ascocarp, which were at first mistaken for fusing nuclei. When the nuclei are preparing for division, the chromosomes tend to become arranged in a group resembling a nucleolus. The nuclei at this stage are of course large, and often, unless well stained and carefully studied, appear to have two nucleoli. When the nucleoli have divided, they often reorganize so close together that after a slight growth they are pressed against each other as in the case of fusing nuclei. Careful study, however, has failed to show any cases in which the nuclear walls were disappearing, and often the remains of spindle fibers could still be distinguished. Even the nuclei resulting from the division of the primary nucleus of the ascus can sometimes be found pressed against each other. Considering the above facts and the increasing amount of negative evidence, it would seem necessary to study the nuclei in all stages, including division, and to distinguish between true and apparent fusions before the fusion of nuclei in the ascogonium can be regarded as proved or even probable. This is particularly true of such an aberrant case as the presence of a second nuclear fusion following the sexual fusion in the life history of the same plant, and it is to be noted that divisions in the ascogonium have not been reported in any of the forms, mentioned above, in which a fusion of nuclei has been described in the ascogonium. In view of what has been said, there would seem to be little reason for thinking that *Leotia* differs from *Monascus* and *Lachnea scutellata* in having a fusion of nuclei in the ascogonium; and so the explanation of the fusion of sister nuclei will probably have to be sought in some other way than by regarding the fusion as simply a vegetative one.

The question may be asked as to whether the relationship of fusing nuclei is of any significance if they are in the same plant

and are derived from a single nucleus with the haploid number of chromosomes. So far as the writer knows, there is no reason for thinking that there is. It is well known in agriculture that self-fertilization causes a diminution in the size and vigor of maize. SHULL (**26**) has shown that ordinary maize is a complex hybrid. If the elementary species are segregated out of the hybrid, self-fertilization has no bad effect, and it would seem that the deterioration of agricultural maize after self-fertilization is due to the segregating out of the smaller elementary species, which when recombined will again produce the more vigorous agricultural variety. According to the Mendelian interpretation, the harmful effect of self-fertilization in other genera is due to the same cause. The value of cross-fertilization for evolution is evident when we remember that it affords a means for trying a new character in a great number of combinations, one of which may finally be especially adapted to its environment. It may be that the persistence of cross-fertilization is due to its value in evolution, and that the presence of self-fertilization in such a relatively small number of the higher plants is due to the fact that such plants had less chance to interchange characters by crossing and so to develop along favorable lines.

It is evident that the above beneficial effects could not be produced by the fusion of distantly related nuclei if these were all in the same plant and were derived from a single nucleus with the haploid number of chromosomes, for even if the potentialities of one of the fusing nuclei were to be changed in some way, the change would probably be inherited by only one-half of the resulting progeny, and the nuclei of these would have the same potentialities as the changed nucleus and there would be no chance for further mixing. The end result would be the same if the nucleus whose potentialities had been changed had divided, and the two daughter nuclei had fused and given rise to the progeny. But even if a change in the fusing nuclei could be thought of as beneficial, there is no reason for thinking that such a change would occur. The work of JENNINGS (**18**) and JOHANNSEN (**19**) seems to show that the germ cells of organisms derived from a single pure individual are very rarely affected, even if the organisms

are subjected to different conditions and a rigorous selection practiced. In view of what has been said, we would not expect the relationship of fusing nuclei to make any difference if they were all in the same plant, and especially if they were all derived from a single nucleus with the haploid number of chromosomes. When therefore the ascogonium and antheridium, as in *Pyronema confluens* (HARPER **16**), came to be derived from a single hypha, it would not seem to be a matter of great significance if the fusion of the nuclei derived from the ascogonium and antheridium should be replaced by the fusion of more nearly related or even sister nuclei, as seems sometimes to be the case in *Leotia chlorocephala*. It may be that the tendency toward the loss of sexual organs which is shown by a large number of the higher fungi is connected with the fact that there is in so many of them no provision for the fusion of nuclei derived from different individuals.

Conjugate division

In the first process of multiplication of asci described in *Leotia chlorocephala* there is a series of conjugate divisions comparable to those in the rusts. When the hook gives rise to a binucleate penultimate cell and a uninucleate ultimate and antepenultimate cell, and then the ultimate cell fuses with the antepenultimate, there result two binucleate cells in which the two nuclei are derived one from each of two pairs of sisters. This is of course the relation that exists in the rusts. The processes in the rusts and in *Leotia* are compared diagrammatically in fig. 47. If in *Leotia* the nuclei divided side by side rather than one in the tip and the other nearer the base of the hypha, and the walls still came in between the sister nuclei, there would result a series of binucleate cells resembling very closely those in the rusts. Such a division in an ascomycete has been described by MAIRE (**20**) in *Galactinia succosa*.

The cells which fuse in the rusts are often derived from separate hyphae, but BLACKMAN (**3**) says that in some cases the fusing cells may be sisters, while OLIVE (**22**) figures two cases in which one nucleus is apparently migrating into an adjoining cell. The fusion of the ultimate and antepenultimate cells in the hooks of

the Ascomycetes is probably vegetative, and its replacement by the fusion of cells of separate hyphae or sister cells would give rise to a process quite similar to that in the rusts. While the above facts suggest a similarity between the Ascomycetes and the rusts, they do not appear to be sufficient to warrant the conclusion that the fusions and conjugate divisions in the two groups are phylogenetically related.

Summary

The ascogenous hyphae of *Leotia* have their origin at the base of the ascocarp, probably from a one-celled ascogonium.

The asci are formed at the tips of the ascogenous hyphae in several different ways. In some cases a hypha forms a typical hook, consisting of a binucleate penultimate and a uninucleate ultimate and antepenultimate cell. In this case the two nuclei of the penultimate cell may fuse to form the nucleus of an ascus, or they may divide and give rise to the four nuclei of another hook. The uninucleate ultimate cell usually grows down and fuses with the antepenultimate cell, after which the nuclei of the two cells may give rise to the nuclei of another hook, or they may fuse to form an ascus. The walls separating the nuclei may fail to be formed without affecting the fate of the nuclei. In this process there is a conjugate division comparable to that in the rusts.

Frequently the ascogenous hyphae do not become markedly bent, and in this case, when the two nuclei in the tip divide, a wall may separate two pairs of sisters. Either of these pairs may divide and give rise to the nuclei of another hook or fuse to form the nucleus of an ascus. Any of the methods described above by which the number of asci is increased may be repeated many times.

The relationship of the nuclei which fuse in a plant like *Leotia* is probably of no significance, since they are all in the same plant and are probably derived from a single nucleus with the haploid number of chromosomes.

The vegetative hyphae form large storage cells in the hymenium. The nuclei in these cells frequently fuse to form a single large nucleus.

The development of the ascocarp indicates that all of its struc-

tures are homologous with those of the Pezizineae, and that *Leotia* is closely related to the Pezizineae.

The writer is greatly indebted to Professor D. S. JOHNSON for valuable suggestions and criticisms, and to Professor C. B. DAVENPORT for courtesies shown him during his stay at the Biological Laboratory of the Brooklyn Institute at Cold Spring Harbor.

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BRIEFER ARTICLES

THREE INTERESTING SPECIES OF CLAVICEPS

(WITH EIGHT FIGURES)

One of the fungi most commonly met in North Carolina occurs in sclerotial form upon *Paspalum laeve* and *P. dilatatum*.[1] Over large areas every plant may bear spikes showing one or more of these sclerotia. In summer they are covered with a yellowish coat of spores, and the fungus has heretofore been variously designated as *Sclerotium Paspali* Schw.,[2] *Sphacelia Paspali* Bornet, and *Spermoedia Paspali* Fr. The species was used extensively by the authors in a physiological investigation,[3] and is well represented in the accompanying photographs (figs. 1 and 2).

FIG. 1.—Sclerotia of *C. Paspali* as seen upon the host.

The abundance of the form and the fact that its perfect stage appeared to be unknown led us to attempt to grow from it an asciger-ous stage. Numerous sclerotia which had wintered out of doors, naturally, were collected from the ground where they had fallen, and were planted on moist earth in glass capsules which were kept at room temperature. After about 20–25 days signs of germination appeared. Soon stalks 5–18 mm. long were developed, and on their ends round heads 1–2 mm. in diameter (fig. 3). By teasing or sectioning, perithecia and asci of the typical *Claviceps* form were found. But most remarkable, two clearly distinct types of perithecia, differing strikingly in size and shape, and bearing spores of decidedly different size, were found. The perithecia of the two forms are shown in figs. 4 and 5.

In the collection of the U.S. Department of Agriculture were found sclerotia from *Paspalum* bearing asci. These proved to be identical with the small-spored form of our own collection. Correspondence between

[1] These species were kindly determined for us by A. S. HITCHCOCK.

[2] FARLOW, Host index, p. 153; also SACC. Syll. Fung. 14:1152.

[3] Variation of fungi due to environment. BOT. GAZETTE 48:1–30. 1909.

Professor ROLFS and the Department of Agriculture, which has kindly been placed at our service, shows that Professor ROLFS at Clemson in 1901 noted the ascigerous stage of *Sclerotium Paspali* Schw. on *P. dilatatum*, and further observed that the ascospores were disseminated largely by beetles, principally of the family Carabidae, which running over the ground came in contact with the spores, and later in seeking a high point from which to fly would run up the culms, over the pistils, and thus bring about infection of the ovaries.

FIG. 2.—Sclerotia of *C. Paspali* upon the host, enlarged.

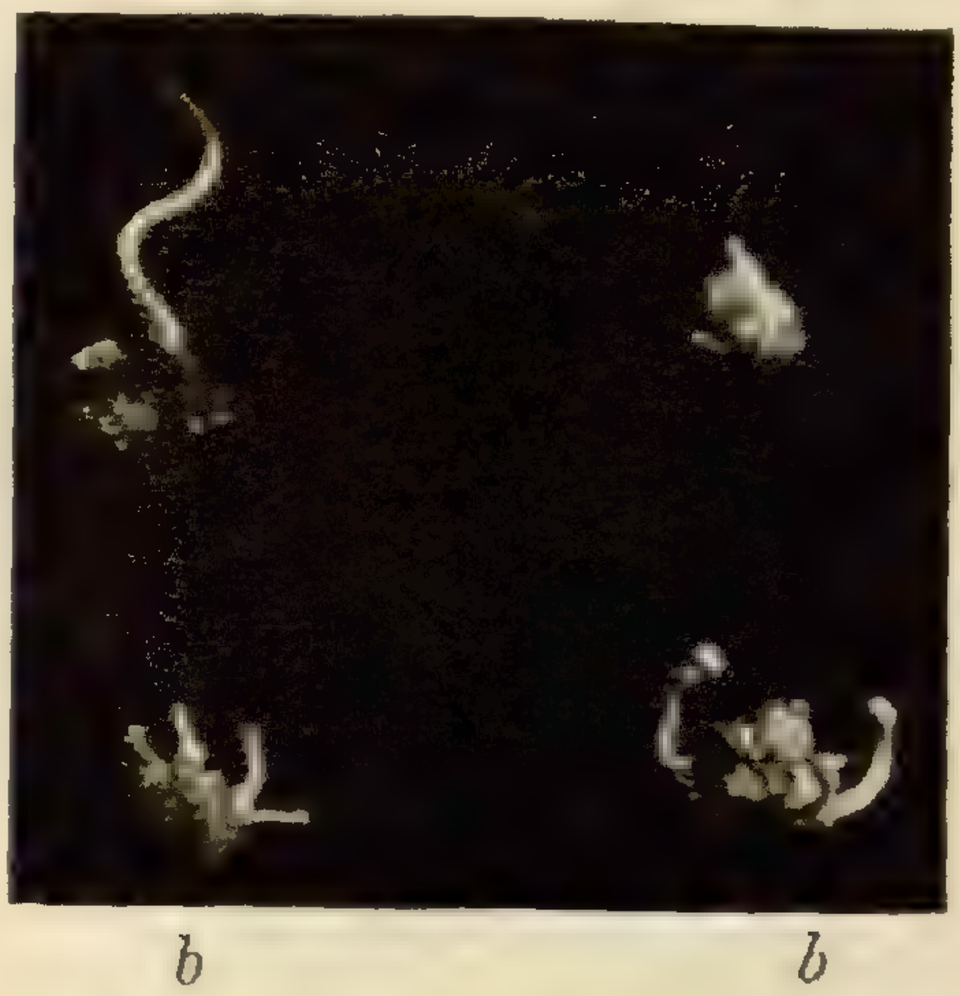

FIG. 3.—Sclerotia of *Claviceps* germinated: *a*, *C. Rolfsii*; *b*, *C. Paspali*.

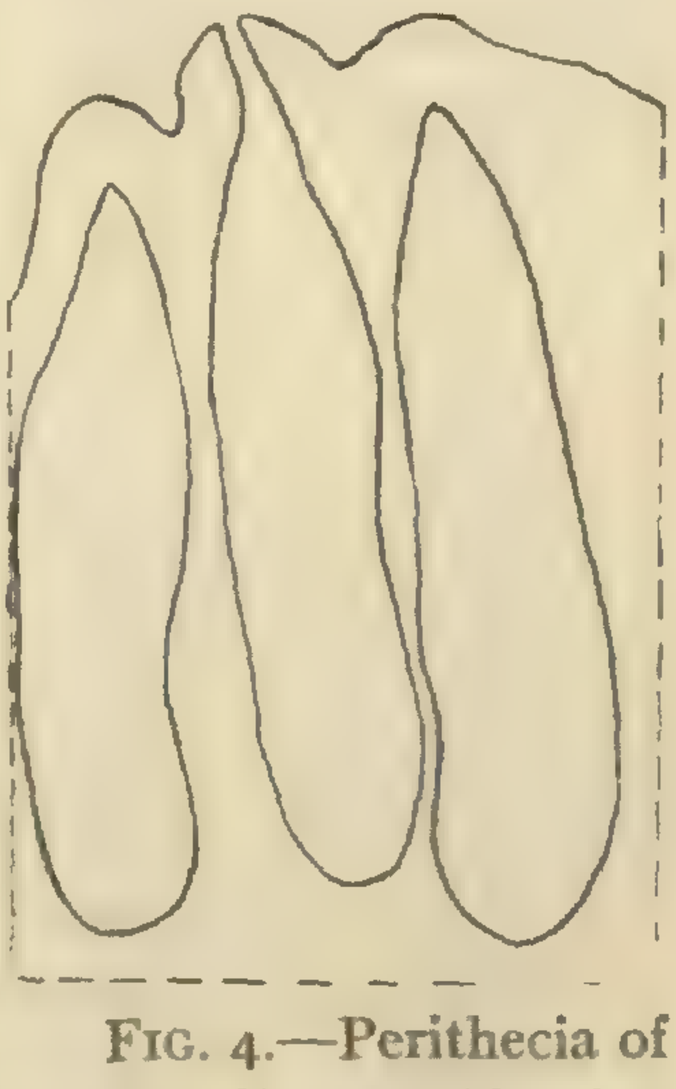

FIG. 4.—Perithecia of *C. Rolfsii*; magnification as in fig. 5.

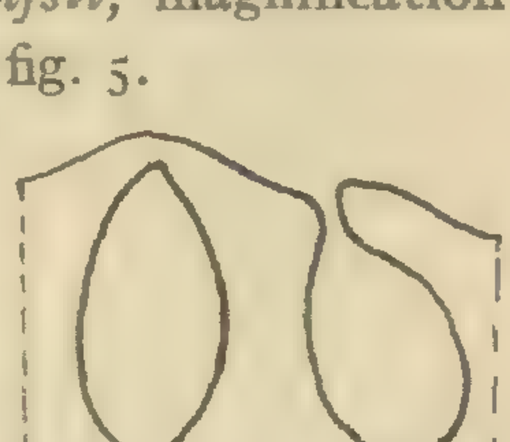

FIG. 5.—Perithecia of *C. Paspali*; magnification as in fig. 4.

Since the two species of *Claviceps* under discussion differ markedly from any heretofore described, and from the only *Claviceps* upon *Paspalum* (*C. lutea* A. Möll.), and from each other in many essential characters, prominently so in length of stipe and size of perithecia and spores, we herewith propose them as new species; the small-spored form as *C. Paspali*; the large-spored form as *C. Rolfsii*. The relation of these two species to *Sclerotium Paspali* Schw. is not definitely known. Both of them are associated with what has heretofore been known as *S. Paspali* Schw. It seems probable, therefore, that two sclerotial forms very closely resembling each other

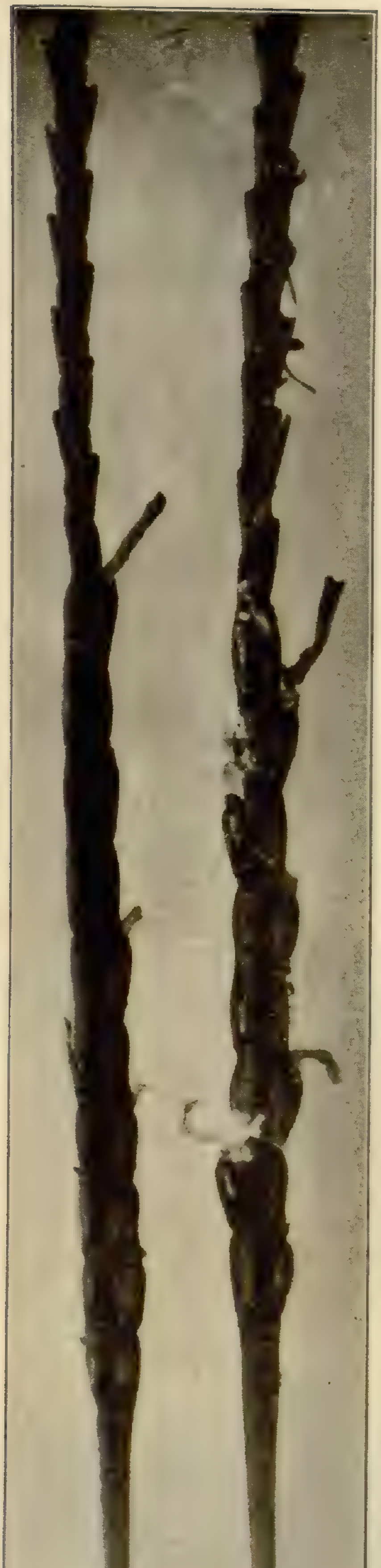

FIG. 6.—*C. Tripsaci* upon the host.

have been included under the one name *Sclerotium Paspali;* but careful cultural studies and infection experiments alone can reveal the true relationship. That *Sclerotium Paspali* really belongs to the form-genus *Sphacelia*, where it was placed by BORNET, is also clear, possessing as it does small ovoid conidia borne upon simple slender stalks.

Claviceps Paspali, n. sp.—Sclerotia yellow to gray, globose roughened when mature, about 3 mm. in diameter; head dull yellow; stipe short to medium, usually not more than 1 cm. long, filiform; perithecia completely covering head, numerous, oval, 340×119 μ; asci cylindrical, 174 μ long; spores filiform, 101×0.5–1 μ.

Claviceps Rolfsii, n. sp.—Sclerotia yellow to gray, globose roughened when mature, about 3 mm. in diameter; head dull yellow; stipe filiform but thicker than in *C. Paspali,* 1–1.5 cm. long; perithecia few in head and mostly upon extreme distal portion, cylindrical ovate, 816×225 μ; asci cylindrical, 375×3 μ; spores filiform, 260–275×0.5–1 μ.

Upon gama grass (*Tripsacum dactyloides* L.) in late summer, and well into winter characteristic fungous growths are often seen protruding from the basal, ovulate portions of the spike, sometimes nearly every spikelet being affected (fig. 6). The structures are white, 12–20 mm. long and about 2–3 mm. thick. Toward their tips they may be browned and more shrunken than in regions near their bases.

Examination of the affected spikelets shows the grain to be absent and its place to be occupied by a light-colored sclerotium approximately the shape of the grain of the

host. In general the appearance is that of a *Claviceps* sclerotium, except that it is pale and soft, the protruding horn being the remnant of the summer stage. Throughout the early part of the season the protruding part bears myriads of straight to lunulate spores, showing strong resemblance to the ordinary lunulate *Fusarium* spore. The internal portion remains sterile throughout the winter. The appearance throughout was so *Claviceps*-like that sclerotia were collected in autumn and wintered in an open-air hibernating house, then planted for germination in the same manner employed with the *Paspalum* sclerotia. After some 20 days the emergence of ascophore stipes was noted, and 5 days later the heads were well developed (fig. 7). A particularly striking feature is the tendency of the stipes to fork and produce two or even four heads upon the same stalk. Teasing or sectioning showed typical *Claviceps* perithecia (fig. 8) and asci. The species seems to be new and we describe it as *Claviceps Tripsaci.*

FIG. 7.—*C. Tripsaci:* sclerotium showing heads and stalks; ×2.5.

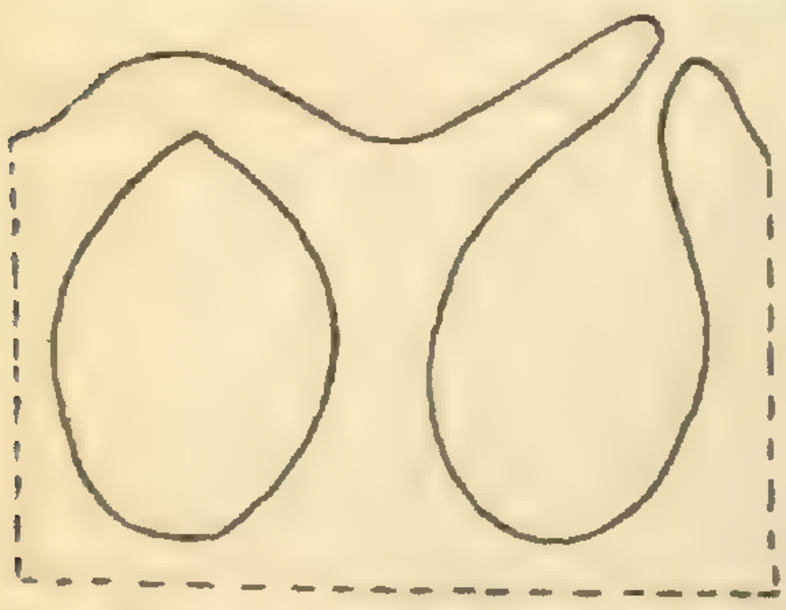

FIG. 8.—Perithecia of *C. Tripsaci;* magnification as in figs. 4 and 5.

Claviceps Tripsaci, n. sp.—Sclerotia smooth, white to dark brown or black, nearly conical, 4–5 mm. in diameter at base; heads gray to grayish white; stipe thick, white to purplish white, 1–1.5 cm. long; perithecia numerous, elliptical in longitudinal section, with a short beak toward the surface of the head, 390×153–187 μ; asci cylindrical, 145–175×2–3 μ; spores filiform, 130 μ long; conidia hyaline, continuous, fusoid to lunulate, 17.4–37.7×2.9–8.7 μ. —F. L. STEVENS and J. G. HALL, *N.C. Agricultural Experiment Station, West Raleigh, N.C.*

CURRENT LITERATURE

BOOK REVIEWS

Iron bacteria[1]

Coming from such authoritative source, this monograph ought to command the earnest attention of workers in the fields of science and of hydraulic and sanitary engineering; containing as it does so much that is of both scientific and practical interest, and embodying within its compass facts and deductions derived from the fruitful though laborious work of some eighteen years. The book is divided into seven chapters with the following titles: (1) The presence and distribution of the iron bacteria; (2) New iron bacteria, and a systematic review of known forms; (3) Pure culture methods; (4) The physiology of iron bacteria, and WINOWGRADSKY'S hypothesis; (5) Other iron organisms; (6) Iron bacteria in relation to the production of bog iron ores; (7) The iron bacteria in their relation to practice: (*a*) rust formation in water pipes, (*b*) iron bacteria and the therapeutic use of chalybeate waters. In this review it will be possible to touch only upon the salient features of the treatise.

The author calls attention to the very wide distribution of the several species of iron bacteria, such as *Leptothrix ochracea*, *Cladothrix dichotoma*, *Crenothrix polyspora*, *Clonothrix fusca*, and *Gallionella ferruginea*, which occur in most bogs, ochre deposits, chalybeate springs, and stagnant waters, and at times in iron water pipes. As is well known, their presence in water pipes may create a veritable nuisance by the plugging of the pipes, or by rendering unfit for manufacturing purposes water that ought to be perfectly clear. It is pointed out as noteworthy that so far no iron bacteria have been recognized growing in sea water. To the six already well known species of iron bacteria, MOLISCH has added three others: *Chlamydothrix sideropus*, *Siderocapsa major*, and *Siderocapsa Treubii*, the last, curiously enough, being found growing on the submerged portions of certain aquatic plants, for example, *Elodea canadensis*, *Vallisneria spiralis*, and *Salvinia auriculata*. Doubtful recognition is extended by the author to certain new forms described by DAVID ELLIS. To obtain pure cultures of the various forms it is recommended that manganese peptone be used in combination with the native water and gelatin or agar, and the cultures should be grown at or about 25° C.

Considerable space is given to a discussion of the physiology of the iron bacteria, dealing particularly with the older and widely accepted theory of

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[1] MOLISCH, HANS, Die Eisenbakterien. pp. vi+83. *col. pls. 3. figs. 12.* Jena: Gustav Fischer. 1910. *M* 5.

WINOGRADSKY that considers iron as a definite necessity for the carrying on of the vital processes of the bacteria. MOLISCH criticizes WINOGRADSKY'S work upon the grounds that that investigator did not work with pure cultures, and chose a bacterium (*Cladothrix dichotoma*) which did not actively store up iron as does one of the commoner forms (*Leptothrix ochracea*), so that his chances for accurate observation and deduction were sadly impaired. On the other hand, MOLISCH has worked with these organisms in pure culture, has demonstrated that they can grow readily enough on an iron-free medium, and that on examination of their protoplasm by microchemical methods no iron can be found. Further, he has shown that the iron bacteria can make use of manganese, as it occurs in water, in a similar way in which they use iron. According to the author, the iron in solution in the water is simply *deposited* in the viscid sheaths of the bacterial filaments in the form of soluble carbonate of iron, and through the action of the atmospheric oxygen it becomes altered to ferric oxid. This ferric oxid is in no discernible way utilized by the bacteria in their vital processes, but in its insoluble state acts as a protecting armor to the delicate protoplasmic filaments, pretty much in the same way as do the deposits or accumulations of silica in the case of the diatoms, or in the case of the epidermal cells of the grasses. When the bacteria use manganese, it is believed that that element is laid down in the sheaths in the form of manganese hydroxid, which under the action of the oxygen of the air is probably altered to manganic acid and finally to manganite.

The disappearance of the bacteria from waters that have been subjected to certain forms of treatment in which the iron is removed, MOLISCH explains in this way. Whether the form of treatment is that of filtration through sand or coke, or by chemical methods, great quantities of soluble organic materials in combination with hydrogen sulfid, ammonia, or carbonic acid are coincidentally removed, and this loss of organic materials is the real element determining the vanishing of the bacteria, inasmuch as it means the utter deprivation of the food supply, the absence of the iron being a matter of entire indifference. In the case of bog waters, the food supply is in the form of humus organic matters that are very readily removed by any method that removes iron. There exist in nature, MOLISCH states, other organisms than bacteria that are capable of fixing iron. These organisms are to be found among the algae, flagellates, and infusoria. His student ADLER has also demonstrated that some of them are able to fix manganese as well as iron. In all cases the *modus operandi* is quite similar to that of the bacteria.

Discussing the nature of the formation of deposits of ochre and bog iron, the author takes no dogmatic stand, but weighs the evidence in the light of the presence or absence of bacteria in material taken from such sources. The finding of bacteria in such deposits argues much for them playing at least a partial rôle in the formation, although it cannot be overlooked that there must be also a chemico-physical precipitation of insoluble iron due to the action of

the atmospheric oxygen and to the alkalescence of bog waters by aquatic plants. In rare instances the iron deposits may be made up almost entirely of the sheaths of the filamentous iron bacteria *Gallionella ferruginea* and *Leptothrix ochracea*. It may also be possible that deposits in which no bacteria may be found may have had their start by the growth of iron bacteria, but later on these may have died out and left no trace of their presence.

In regard to the formation of iron rust in water pipes, the author is in accord with the observations of the English investigator BROWN, and others, who believe that very often the incrustations of rust on the inner surface of the pipes may begin in areas accidentally left bare in the usual tarring process, and ferric oxid is formed by the action of the water entirely apart from the presence of iron bacteria, as the author himself has time and again demonstrated. It must be remembered, however, that where the presence of iron bacteria can be unequivocally established, there must occur the favorable combination of both soluble iron and organic food material; lacking the latter in sufficient quantity, no iron bacteria can gain a foothold.

MOLISCH very timely points out that much of the chalybeate waters bottled for medicinal purposes is worthless on account of the precipitation of the iron in insoluble form (ferric hydrate). This may be caused in one of two ways: (1) by the action of the air acting on the soluble iron carbonate, and (2) by the activities of one or other of the iron bacteria. This latter fact is established beyond a doubt, inasmuch as ADLER has cultivated iron bacteria from the waters of several chalybeate springs, and by the addition of various antiseptics has delayed the action of precipitation of the iron by inhibiting the growth of the bacteria. In practice such waters are recommended to be treated by filtration or by sterilization by heat.

The monograph is supplied with a full bibliography of the subject, and is plentifully illustrated with colored plates, original drawings, and photographs. The work constitutes a most valuable contribution to our knowledge of these peculiar and interesting microorganisms.—NORMAN MACL. HARRIS.

The morphology of gymnosperms[2]

In the present handsome volume the authors have more than doubled the size of their book on the same subject published almost a decade ago. It is a significant fact that the "fossil gymnosperms," relegated to an all too brief chapter in the earlier edition, are now distributed in accordance with their evolutionary sequence, and adequately and even copiously treated. The volume begins with the Cycadofilicales, as they are appropriately dubbed, in preference to the earlier and less suitable appelations Cycadofilices and Pteridospermeae. This group of gymnosperms, which has clearly emerged

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[2] COULTER, J. M., and CHAMBERLAIN, C. J., Morphology of gymnosperms. pp. xi+458. *figs. 462*. Chicago: The University of Chicago Press. 1910. $4.10, postpaid.

from the paleobotanical limbo only within the decade, is given full consideration from every standpoint, and the account is made clearer for the general reader by an admirable summary of the general principles of fern anatomy. Next follow the Bennettitales, a group which American science has done so much to rescue from oblivion. In this as in the preceding chapter the authors have illustrated their account with good figures from original sources, and here we find the work of WIELAND, WILLIAMSON, and NATHORST freely drawn upon, just as SCOTT, OLIVER, KIDSTON, and POTONIÉ furnish the figures for the first chapter on the Cycadofilicales.

The treatment of the Cycadales is particularly full, as might be expected, in view of the special interest of the Chicago laboratories in the group. The illustrations comprise not only the gametophytes, but also the anatomy, which is more comprehensively dealt with in this instance than in the case of any of the other gymnosperms. This chapter must rank as perhaps the best in the volume. The Ginkgoales occupy about 35 pages. An interesting illustration here is a tone print of the identical tree from the botanic garden of the University of Tokyo, in the seeds of which HIRASÉ made the surprising discovery of spermatozoids.

The Coniferales naturally receive more attention than any of the older gymnosperms, since they are the prevailing naked-seeded plants of our epoch, and moreover are the exclusive representatives of the phylum in temperate climates. In the 140 odd pages devoted to the Coniferales, the authors discuss the order under the appelations customary in systematic accounts. It seems desirable as soon as possible to get rid of the inapposite and cumbersome appelations Pinaceae and Taxaceae, inherited from the taxonomic side, and replace them by other terms more in accordance with evolutionary lines in the Coniferales. Perhaps the time is not yet entirely ripe for that to be done. Although the conventional bifurcation of the Coniferales is adopted, the authors do not fail to discuss the hypothesis recently put forward by SEWARD, PENHALLOW, and the reviewer as to more appropriate groupings. It is recognized that the araucarian conifers stand in a group by themselves as compared with the Abietineae, Taxodineae, and Cupressineae. The authors even go so far as to grant, what seems inadmissible from the paleobotanical side, that the Araucarineae and pinoid conifers may have had an altogether separate origin from the Cordaitales. Nothing can apparently be clearer than that the earliest remains which can be referred either to araucarineous or abietineous affinities, have all the characteristics of conifers. The treatment of the coniferous series is particularly worthy of praise for its thoroughness and many-sidedness. The bane of morphology in the past has been the setting up of evolutionary hypotheses based on the consideration of facts of a single kind. This error has certainly been avoided here. The external habit, the spore-producing members, the vascular anatomy, the sporangia, the gametophytes, and the history or paleontological record of the group have all been considered. The result is one which,

although not without prudent reservations, is clear and along stimulating and evolutionary lines, with a due emphasis of principles and the avoidance of meaningless facts. What is most to be commended, and unfortunately a rare feature in botanical textbooks, is the recognition that stable results in connection with plant evolution can be built only on the firm basis supplied by the record of the rocks. Perhaps the only criticism which might be made of the long chapter on the Conifers is that it does not include among its many and good illustrations some of the anatomy of the gro[illegible]pecially as the importance of this phase of the subject is clearly and [illegible] the inne[illegible]y recognized in the text.

[illegible]ual tarring [illegible]

About 40 pages are given to that fascinating [illegible]part from [illegible]spite of many recent additions to our knowledge, enigmatical group, [illegible] Gnetales. Presenting as it does so many characters, which ally it both with [illegible] gymnospermous and angiospermous seed plants, it is at once [illegible] and the despair of the morphologist. The conclusion is reached that the Gnetales rather represent a line of development from the same ancestry as the angiosperms, than a primitive group from which the higher seed plants have directly taken their origin. The authors seem to look with some degree of tolerance at least on the view, which has originated in recent years from added knowledge of the floral structure of the Bennettitales, to the effect that the angiosperms and Gnetales are an offshoot of the cycadophyte stock. This view of relationship rests entirely on the enigmatical inflorescence of the Bennettitales, and appears to have no support from a consideration of the structure of the gametophytes or the internal anatomy. While entertaining the possibility of a Bennettitean origin of the Gnetales, the authors at the same time suggest a possible derivation from the Coniferales. This is perhaps a more fruitful hypothesis, which may be justified when we possess some real knowledge of the past history of the group.

The volume reviewed is a masterly treatment of our present knowledge of the gymnosperms, and resumes in a particularly clear and happy way, from every standpoint, the evidence as to their structure, affinities, history, and evolution. It is vastly creditable to American morphology, and the statement may safely be made that there is nowhere in existence, at the present time, a general account of the group which is so judicial and authoritative, without being dull, hazy, or uninteresting. It follows of course that it is indispensable to every student of this important group of plants.—E. C. JEFFREY.

Vegetation der Erde

The ninth volume of ENGLER and DRUDE'S monumental work on the vegetation of the earth forms one of a series of monographic treatises that is to deal with the geographic features of the African flora.[3] Although the volume

[3] ENGLER, A., and DRUDE, O., Die Vegetation der Erde. IX. ENGLER, A., Die Pflanzenwelt Afrikas insbesondere seiner tropischen Gebiete. Band II. pp. xi+460. *pls. 16. figs. 316.* Leipzig: Wilhelm Engelmann. 1908. *M* 27 (subscription price *M* 18).

here under consideration is the first of the African series to make its appearance, it is logically the second, and will so stand in the completed work. The first volume is to give a general picture of the plant world of Africa, together with a survey of the ecological conditions. The following three volumes are to present detailed descriptions of the characteristic plants, especially of tropical Africa. The final volume is to deal with the plant formations and floral provinces.

For many years DRUDE and a number of collaborators have energetically exploited the flora of Africa, especially that of the German possessions. The taxonomic part of the Cyperaceae great undertaking have been presented from time to time, and now special interest contemplated in these volumes a general summary of the large features of the African vegetation. The volume noted here gives an account of the pteridophytes, gymnosperms, and monocotyledonous angiosperms. For each there is given a general account of its distribution and importance in Africa, following which is a more detailed description of the more important genera and species. The great wealth of illustrations, many of which are reproductions from photographs, makes this work the best source of ready information concerning the plants of Africa. Among the pteridophytes the Polypodiaceae play much the largest part. The gymnosperms are restricted to three genera each of cycads, conifers, and Gnetales. The grasses, which are presented by PILGER, have an immense number of forms, many of which are of great phytogeographic importance; the chief treatment of this great family is by plant formations rather than by taxonomic relationships. The numerous Cyperaceae are mostly hydrophytes. The palms, of course, are numerous, and are very characteristic of certain formations. The aroids are well developed, though less than in other tropics, and the epiphytic orchids are far less numerous and beautiful than in tropical America and Malaysia. The Liliaceae occur in great numbers and variety, the aloes in particular having a large display in xerophytic regions. Phytogeographers will await with eagerness the remaining volumes of this work.

In 1898 PAX issued the second monograph of ENGLER and DRUDE'S *Vegetation der Erde*, presenting the general features of the vegetation of the Carpathian Mountains. There has appeared a second volume, which takes up certain detailed features of the same interesting region.[4] The first part considers the fossil flora of the Carpathians, especially that of the Tertiary and Post-Tertiary. The Tertiary flora is Upper Miocene, and much resembles the present Mediterranean flora, and as elsewhere in Europe is rich in forms that are now confined to America. It is interesting to note that in the warmer eastern Carpathians there are still some species which have remained as relicts from the Miocene. Since the ice age there has been in the western Carpathians

[4] ENGLER, A., and DRUDE, O., Die Vegetation der Erde. X. PAX, F., Grundzüge der Pflanzenverbreitung in den Karpathen. Band II. pp. viii+321. *map 1. figs. 29.* Leipzig: Wilhelm Engelmann. 1908. *M* 27.

a succession of forest forms, the birch and pine entering soon as pioneers; there followed then in turn the oak, the spruce, and finally the beech. The second part opens with a treatment of Carpathian genera which show slight variation, or which on the other hand are strikingly variable; this study results in interesting deductions of evolutionary importance, There follow a consideration of phenological phenomena, an account of the cultivated plants of the Carpathians, and a phytogeographical description of the thallophytes and bryophytes, which too often are ignored in such treatises. The treatment of the thallophytes is brief, owing to inadequate knowledge of their distribution, but the account of the bryophytes is more satisfactory. The western Carpathians are richer in bryophytes than the eastern Carpathians, owing to the greater rainfall and humidity. The third and final part treats in detail the particular features of the different districts of the Carpathians.—HENRY C. COWLES.

Plant anatomy

A second edition of STEVENS' *Plant anatomy*[5] has appeared three years after the first edition, which was reviewed in this journal.[6] That review stated fully the purpose and method of the book, so that only the notable new matter in the second edition needs notice here. It consists of a chapter of 38 pages on reproduction, and has been made imperative by the recent rapid development of plant-breeding as a science, involving as it does the fundamental principles of heredity. Professor STEVENS outlines first the mechanism of sporogenesis and of fertilization as now understood, and then presents in a clear and practical way the conclusions that have been reached by the application of MENDEL'S law. As said in the previous review, Professor STEVENS is an excellent teacher, and therefore, by text and apt illustrations, he has made an obscure region as luminous as it can be made for an elementary student.

As an elementary text on physiological anatomy, in which tissues and their functions are interwoven in their presentation, this volume is unique. It is not the new vascular anatomy, with its phylogenetic motive; or the old anatomy, with its deadness of detail; but the old "skeleton" animated by physiology and ecology rather than by evolution.—J. M. C.

MINOR NOTICES

Das Pflanzenreich.—Part 41[7] consists of a monograph of the Garryaceae, Nyssaceae, Alangiaceae, and Cornaceae by Dr. WALTER WANGERIN. In

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[5] STEVENS, WILLIAM CHASE, Plant anatomy, from the standpoint of the development and functions of the tissues, and handbook of micro-technic. Second edition. pp. xv+379. *figs. 152*. Philadelphia: P. Blakiston's Son & Co. 1910. $2.

[6] BOT. GAZETTE **46**:306. 1908.

[7] ENGLER, A., Das Pflanzenreich. Heft 41 (IV. 56[a]; 220[a, b]; 229). Garryaceae, Nyssaceae, Alangiaceae, Cornaceae, von WALTER WANGERIN. pp. 17, 19, 24, 110. *figs. 5 (26), 6 (47), 4 (38), 24 (193)*. Heft 42 (IV. 147). Euphorbiaceae-Jatropheae, von F. PAX. pp. 148. *figs. 45 (155)*. Leipzig: Wilhelm Engelmann. 1910. *M* 9.20; *M* 7.40.

these four families the author recognizes 15 genera and about 140 species. New species are published in *Garrya* and in *Alangium;* and several recently described species of *Cornus* have been incorporated and redescribed. The work is comprehensive, conservative in generic and specific limitations, copiously illustrated, and provided with excellent keys; it should serve as a valuable and authentic guide in the taxonomic study of plants belonging to these natural groups.

Part 42 embraces an exhaustive taxonomic treatment of the Euphorbiaceae-Jatropheae by Professor F. PAX. The tribe comprises 12 genera, and to these are referred 196 species, of which 43, or approximately one-fourth, are new to science. One new genus is included, namely *Neojatropha* of eastern tropical Africa, where it is at present represented by two known species. A second new genus (*Ritchieophyton*) is suggested and included in the key to the genera of the tribe, but publication of it is withheld for a subsequent fascicle dealing with this family. The group is treated in a masterly way, and numerous carefully executed original illustrations amplify the lucid text. Of considerable interest is the brief section dealing with geographical distribution. Seven of the twelve genera are exclusively American, while five (including *Ritchieophyton*) are paleotropic; and *Jatropha*, the largest of all the genera, extends throughout the equatorial belt. The two great centers of distribution of these plants in America are (1) in the region from Central America southward to Brazil and Paraguay, and (2) independently, in the West Indies.—J. M. GREENMAN.

A new flora of Congo.[8]—The present volume records all flowering plants of the Congo known up to the end of 1908, and includes a limited bibliography, citation of exsiccatae, and the vernacular names in many instances. The flora embraces a total of 3546 recognized species, of which 2826 belong to the dicotyledons, 717 to the monocotyledons, and 3 to the gymnosperms. The last group is represented by *Gnetum africanum* and two species of *Encephalartos*. The main elements of the flora, as represented by leading families, are as follows: Leguminosae (415 species), Rubiaceae (299), Orchidaceae (152), Compositae (148), Euphorbiaceae (144), Cyperaceae (139), and Gramineae (132). A very interesting tabulation is given showing the growth of our knowledge of the flora from 1896 to 1908. The work is well indexed, but is entirely without keys to genera or species. Brief keys leading to the species, particularly in the case of the larger genera, would have added considerably to the usefulness of the book.—J. M. GREENMAN.

Paleobotanical literature.—JONGMANS[9] has begun the publication of a very useful and a most laborious series, presenting a complete and well-organized

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[8] DURAND, THÉOPH. ET HÉL., Sylloge Florae Congolanae. Bull. Jard. Bot. Brux. **2**:1–716. Bruxelles: Maison d'édition A. Castaigne. Albert de Boeck, Successeur. 1910.

[9] JONGMANS, W. J., Die palaeobotanische Literatur. Vol. I. pp. iv+217. Jena: Gustav Fischer. 1910. *M* 7.

bibliography of paleobotany. The first volume contains the titles of 1908, and is divided into two sections: (1) an author list (pp. 17), which includes 309 entries; and (2) a subject list (pp. 200), by which one may find at once any plant referred to. The number of titles is increased by the fact that the list includes many papers on living forms which are related in some way to the interpretation of paleobotanical material. In these days, when paleobotany is becoming such a necessary part of morphology, such a volume has become indispensable.—J. M. C.

A revision of the genus Eucalyptus.—The title-page and index received recently completes the first volume of *A critical revision of the genus Eucalyptus* by J. H. MAIDEN.[10] In this volume the author treats 40 species, giving detailed descriptions, synonomy, distribution, and much supplementary information; these species and their known varieties and forms are illustrated by 48 admirable plates. The work is an exhaustive and authoritative treatment of this highly interesting and economically important group of plants, and it is a pleasure to note that it is being continued; the first part of the second volume, containing nine species and four plates, has already been issued.—J. M. GREENMAN.

Illinois State Academy of Science.—The third volume (1910) of Transactions contains the following botanical papers: The vegetational history of a blow-out (abstract), by H. A. GLEASON; Preliminary account of the forest successions on Isle Royale, Lake Superior (abstract), by W. S. COOPER; The forest associations of northwestern Illinois, by H. S. PEPOON.—J. M. C.

NOTES FOR STUDENTS

Plant diseases.—BANCROFT[11] has studied the life history of *Cladosporium herbarum* and finds that this fungus, known to be common on dead leaves, is connected with a parasitic stage which from its fructification would be classed in the form genus *Hormodendron*. The *Hormodendron* form makes holes in the leaves of many plants, among which are cucumber, melon, and cabbage. It is mentioned as epidemic in cucumber leaves. The holes are said not to be formed by the drying and falling out of areas of tissues, as in leaf-spot diseases. In this case the perforations occur from the first and increase in size, often running together so as to form large irregular holes. The margins are surrounded by a narrow line of dead brownish tissue. From the tissues surrounding the holes conidiophores of *Hormodendron* appear and produce branched chains of conidia. In cultures from these chains, conidia of *Hormodendron* were at first produced, but as the cultures became older only those of *Cladosporium* were formed.

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[10] MAIDEN, J. H., A critical revision of the genus *Eucalyptus*. 4to. pp. 349. *pls. 48*. Sydney: William Applegate Gullick. 1903–1909.

[11] BANCROFT, C. K., Researches on the life history of parasitic fungi. I. *Cladosporium herbarum* Link. Annals of Botany **24**:359–372. *pl. 1*. 1910.

It was found also that on dead or dying leaves infected with *Hormodendron* the conidia of that form gave way to fructifications of *Cladosporium*. It seems, therefore, that during the actively parasitic life of the fungus *Hormodendron* conidia are formed, but at the end of the growing season *Cladosporium* develops on the dead and fallen leaves. The conidiophores of *Cladosporium* arise from a sclerotium-like mass of fungous cells. The author finds that the cells of this sclerotium retain their vitality through the winter and give rise to conidiophores of *Cladosporium* in the spring. The disease is probably propagated by means of these sclerotia and conidia.

In order to describe the means by which some of the parasitic fungi whose ascospores are either not often found or are entirely unknown to persist through the winter, EWERT[12] has studied the effect of low temperature on the conidia of several species. The pycnidia of *Mycosphaerella sentina* Kleb. on fallen pear leaves left exposed during the winter were found to contain numerous conidia capable of germination during all the months of winter and as late as June, when new infections of the fungus appeared in the orchards. The temperature during the winter ranged as low as −22°.2. Infection experiments with these conidia were not successful, but this the author attributes to faulty methods of manipulation. Infections with other conidia which had been exposed to low temperatures for a short time were successful. The conidia of *Pseudopeziza Ribis* Kleb. were also shown to retain their vitality through the winter. Conidia of *Fusicladium pirinum* and *F. dendriticum* subjected to low temperatures once or several times were still capable of germination, although in this case the matter is of less importance, since both of these fungi form ascospores regularly, and moreover have a perennial mycelium.

BROOKS and BARTLETT[13] report on two diseases of gooseberry bushes caused by *Botrytis cinerea* and *Cytosporina Ribis*. The first indication that plants are attacked by *Botrytis* is the wilting of one or more branches. Later the basal parts of such branches show great numbers of conidiophores of *B. cinerea* arising from sclerotia situated just outside of the woody cylinder. At this time it is found that the pith, wood, and bast are filled with mycelium. The fact that the wood is infected is particularly interesting, as *Botrytis* generally attacks only the soft parenchymatous tissues. It appears, however, that in this case lignified walls are not affected by the fungus, which makes its way through the vessels, and passes from cell to cell through the pits. The composition of the lignified tissues appears not to be changed. The food substances of the medullary rays are used up, but nothing is said of the contents of the wood parenchyma. Infections were produced by inserting into wounds

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[12] EWERT, R., Die Ueberwinterung von Sommerkonidien pathogener Ascomyceten und die Widerstandsfähigkeit derselben gegen Kälte. Zeitschr. Pflanzenkrank. **20**: 129–141. *figs. 2.* 1910.

[13] BROOKS, F. T., and BARTLETT, A. W., Two diseases of gooseberry bushes. Ann. Myc. **8**:167–183. *pl. 1.* 1910.

small pieces of grape juice gelatin, in which the mycelium of the fungus was growing. Inoculation experiments with spores were not successful. The authors suggest that plants in nature may become infected through aphis punctures, the honey dew furnishing a means for the germination of the spores, or by means of frost injuries, or by accidental wounds made in picking the fruit. Since infection by any of these means was not demonstrated, and the authors' own infection experiments with conidia were unsuccessful, these suggestions would be more convincing if supported by more experimentation and less theory.

The disease produced by *Cytosporina Ribis* resembles in its general effects that caused by *Botrytis*. The infection takes place through a wound, as is shown by the universal occurrence of an old scar or dead stump at the point from which the disease spreads. Cross-sections of infected branches show that the wood is brown and discolored except for a lighter sector-shaped area. The wood is permeated with hyphae which, unlike those of *Botrytis*, are able to dissolve the lignified elements of the stem. The progress of the mycelium is accompanied by the formation of wound-gum which accumulates in the cells and vessels. The gum, at least in the wood parenchyma and medullary rays, appears to be formed from the starch. It seems that the accumulation of gum occurs only within the cells and does not involve the destruction of whole areas of tissues, as in most cases of gummosis.

McALPINE[14] reports a number of laboratory experiments with *Phytophthora infestans*, among which is an attempt to determine the possibility of destroying the mycelium in infected potato tubers without destroying the life of the tubers. Slices taken from diseased tubers were subjected to a temperature of 49° for four hours, and the fungus was found to have been destroyed. Afterward seed potatoes were subjected to the same heat and were found to sprout freely, hence the conclusion that seed potatoes can be thoroughly disinfected in the way described. It seems that the method should at least have been given a more extended trial to justify the conclusion, for it is not unlikely that whole tubers would be injured if subjected to that temperature long enough to kill the mycelium in their interior, although the mycelium might be readily killed in thin slices. The author does not state whether the slices in which the mycelium was actually killed retained their vitality through the treatment or not. Neither does he state that the seed potatoes used were diseased before the treatment and free from disease afterward.—H. HASSELBRING.

The species of Penicillium and Aspergillus.—The forms of Fungi imperfecti grouped under the name *Penicillium*, on account of their omnivorous habits, have served as subjects for numerous physiological investigations, but as a rule little attention has been given to the determination of the species in

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[14] McALPINE, D., Some points of practical importance in connection with the life history stages of *Phytophthora infestans* (Mont.) DeBary. Ann. Myc. **8**:156–166. *pl. 1.* 1910.

this group. The genus has been as repellent to the systematist as it has been attractive to the physiologist. With the exception of the work of DIERCKX, only a brief abstract of which seems ever to have been published, there has been no effort to disentangle the mixture of forms of this genus. The efforts of THOM[15] toward clearing up this tangle and making possible the identification of forms will be welcomed, therefore, by botanists and especially by plant physiologists, who are now enabled to connect certain physiological activities with definite species.

The plan of the work has been to carry out on different media of known composition series of cultures of all forms obtainable, and base the distinction of species upon differences in the forms and in their reaction upon the media under similar environment. The method is essentially that which has enabled bacteriologists to classify the enormous number of forms with which they deal. By this method it is shown that the same species differs greatly in morphological characteristics and physiological reactions when grown on different media. Species that resemble each other upon one medium show marked differences upon other media. The characters of the plants are constant for each medium upon which they are grown. The cultural work of this investigation has extended over more than four years, and has resulted in the accumulation of many valuable physiological data which are conveniently tabulated at the end of the paper.

In the systematic part of the work 36 species and 3 varieties are carefully described and their reactions upon various culture media given. Of these, 13 species and 3 varieties are described as new; 9 are described under numbers, since the author feels that their characteristics are not yet sufficiently well known to warrant giving them names. Camera lucida drawings showing the modes of branching of the conidiophores, and other diagnostic characters are given for 33 species and the 3 varieties. The number of species described probably represents a large proportion of the known species of *Penicillium*. Many of them are described as new, but it may be that of these some are included in the 80 odd species in the *Sylloge*, for it is practically impossible, as the author has found in spite of the most painstaking attempts, to identify plants with older descriptions or herbarium material.

A work similar in nature, but far less in extent, was done by MANGIN[16] for a small group of molds of the genus *Aspergillus*. He takes up the forms confused under the name *Aspergillus glaucus*, securing 23 collections from various sources and subjecting them to comparative study under various conditions. Their reactions to different temperatures and to different nutrient solutions enabled him to separate the forms into few groups, the reactions of whose

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[15] THOM, CHARLES, Cultural studies of species of *Pencillium*. Bur. Animal Ind. Bull. 118. pp. 109. 1910.

[16] MANGIN, L., Qu'est-ce que l'*Aspergillus glaucus?* Ann. Sci. Nat. Bot. IX. 10:303–371. *figs.* 15. 1909.

members were constant for the same media or temperatures. He shows that characters of the conidia are not sufficiently constant for the differentiation of species; the form and dimensions of the ascospores, however, are useful as diagnostic characters of species. Four species confused by authors as *Aspergillus glaucus* are described and figured; two of these are new. A variety *violaceum* is added under *Eurotium herbariorum*, and characters are given to separate these forms from two other members of the same group, *A. Oryzae* and *A. flavus*.—H. HASSELBRING.

Fossil Osmundaceae.[17]—In this final contribution on the fossil Osmundaceae, the authors bring to a conclusion their investigations and summarize their results for the whole series. The present memoir deals with a new stem, *Osmundites Kolbei*, from the Jurasso-Cretaceous (Wealden) of Herbertsdale, Cape Colony. The softer tissues are stated to be almost entirely destroyed before fossilization, so that only the fibrovascular and scelerenchymatous systems are left. The stem is much flattened and generally in a condition of extreme collapse. The authors state that the fibrovascular ring is so much flattened that the opposite sides are sometimes in contact with each other. They omit to state, a matter of the utmost importance in connection with their conclusions, clearly shown by their fig. 1, that the condition of maceration is so extreme that the central cylinder has not only collapsed but has been burst open and distributed throughout the cross-section of the stem. It is not surprising, in view of the extreme decay and displacement presented by their material, that they find tracheids and masses of tracheids scattered in the central substance lying in the midst of the displaced fibrovascular strands. The authors express the conviction "that there is no doubt that the tracheal elements are true and real constituents of the central tissue." It is unfortunate that they have not demonstrated the accuracy of their interpretation by figures of transverse sections on a sufficient scale of magnitude of the stelar tissues. An unprejudiced anatomist would scarcely admit the accuracy of their statements on the evidence they submit. From this highly disintegrated stem it is not surprising, in view of their previous statements, that they draw the conclusion that the central tissue of the osmundaceous stele was originally composed of tracheids, and that hence the pith in this family is a derivative of the fibrovascular tissues. The authors make the discovery, anticipated by Mr. SINNOTT in the case of the living Osmundaceae, that foliar gaps apparently absent in *Osmundites Kolbei* are in reality present. Finally, they draw up a table of the osmundaceous forms investigated by them, which shows clearly that the protostelic representatives are of more ancient origin, so far as the available geological record goes, than whose with a developed pith. Their reasoning in regard to the medullate forms is not so conclusive, since they mention three species, *O. Gibbiana*, *O. Kolbei*, and *O. skidegatensis*, from not very

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[17] KIDSTON, R., and GWYNNE-VAUGHAN, D. T., Fossil Osmundaceae. IV. Trans. Roy. Soc. Edinburgh **47**[3]:no. 17. 1910.

different geological levels, Lower Cretaceous and Upper Jurassic, as proving their hypothesis that the pith of the Osmundaceae is of stelar origin and that the medullate forms are an ascending series, beginning with species which have a pith but no foliar gaps separating the collateral bundles, and ending with those in which the bundles are concentric and separated by widely patent gaps. So far as the testimony goes, which they have brought forward in their various memoirs, this hypothesis appears to bear a surprising resemblance to a confession of faith, since it is essentially the substance of things not seen but hoped for.—E. C. JEFFREY.

Parasites and xeno-parasites.—The extensive investigations of CANNON[18] upon the root habits of desert plants has added *Orthocarpus purpurascens* and two species of *Krameria* to the list of semiparasitic plants. *Orthocarpus*,[19] the first to be reported, is an annual of small size, united by its roots to a considerable variety of hosts, of which most are also annual in habit. *Krameria canescens* and *K. parvifolia*, two shrubby desert plants, were formerly taken to be autophytic, and the present study seems to show that they have not advanced far in parasitism. The seeds germinate readily irrespective of the presence or absence of the host plants, and the seedlings are capable of independent existence for an indefinite period, and yet when associated with possible hosts the root tips of *Krameria* organize haustoria penetrating the roots of the host and forming therewith close vascular connections. *Krameria parvifolia* has been found on *Parkinsonia microphylla* only, but *K. canescens* has a variety of hosts, being most frequently associated with *Covillea tridentata*. These parasites show but few of the atrophies or alterations usually accompanying dependent nutrition.

In making a study of the conditions which may have led to the development of parasitism, MACDOUGAL[19, 20] has succeeded in uniting various plants, so that the one lived parasitically upon the other for more than two entire seasons. Various species of cactus were usually chosen as hosts, *Echinocactus* and the giant *Cereus* figuring most conspicuously in this rôle, while the "xeno-parasites" included the Mexican grape, agave, various cacti, and other succulent plants. After the union of the host and parasite was effected, there appeared in the development of the latter the atrophies and reductions characteristic of parasites. It appears that the relative acidity of the sap of the two plants has no part in determining their potentialities as parasite and host, but for the one to draw its nutrition from the other the latter must possess sap of a lower osmotic activity than the former, although not all plants thus related

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[18] MACDOUGAL, D. T., and CANNON, W. A., The conditions of parasitism in plants. Publication no. 129, Carnegie Institution of Washington. 1910.

[19] CANNON, W. A., Parasitism of *Orthocarpus purpurascens*. Plant World **12**: 259–261. 1909.

[20] MACDOUGAL, D. T., The making of parasites. Plant World **13**: 207–214. 1910.

are capable of symbiosis, there being other unknown limiting factors.—GEO. D. FULLER.

Fertile and sterile strains of Hymenomycetes.—Miss WAKEFIELD[21] has made a study of the conditions influencing the formation of fruit-bodies of *Schizophyllum commune* and *Stereum purpureum*, which were grown in pure cultures on bread and gelatin or agar media. The most interesting fact brought out by the work is that a disposition or tendency to form fruit-bodies is characteristic of certain strains, while others have a strong tendency to remain sterile. Of thirteen colonies of *Schizophyllum commune* obtained from single spores from various sources, two formed fruit-bodies readily, while the others remained sterile or showed only a slight tendency to fruit. When propagated by the transplanting of bits of mycelium to new nutrient media, the strains maintained their peculiar characteristics with regard to fruiting. *Stereum purpureum* behaved in a similar manner. Although the capacity for fruiting is thus a characteristic predetermined in the spore, the actual production of fruit-bodies is dependent upon certain internal conditions which were studied to some extent. In a moist atmosphere, depressing transpiration, only vegetative growth appears. Absence of light also is said to inhibit the formation of normal fruit-bodies in *Schizophyllum*. Certain other factors appear to act as direct "releasing stimuli." Thus the sudden withdrawal of nutriment leads to the production of fruit-bodies. Even some of the sterile strains show a tendency to fruit under proper conditions of transpiration and nutrition, indicating that the line between sterile and fertile strains may be after all largely a matter of response to environment.—H. HASSELBRING.

Sand dunes of New Zealand.—In preparation for efforts at dune reclamation, COCKAYNE[22] has prepared a report upon the sand dunes of New Zealand. They cover an area of over 500 square miles, with a general height of 20–50 feet, but occasionally attaining a maximum height of 300 feet. A general summary of their geological character and history is followed by a consideration of the disturbing effect of man's burning and grazing operations. Many dunes that had long been entirely fixed have thus been revivified by advancing civilization. A discussion of the ecological factors involved brings to light the interesting conclusion that the amount of precipitation affects the dune flora very little, areas with an annual rainfall of 100 inches having the same vegetation as others with only 25 inches. A very large number of cloudy and rainy days, however, does modify the xerophytic character of the dune plant associations. The sand-building and sand-collecting plants are

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[21] WAKEFIELD, MISS E., Ueber die Bedingungen der Fruchtkörperbildung, sowie das auftreten fertiler und steriler Stämme bei Hymenomyceten. Naturwiss. Zeitschr. Forst. u. Landwirtsch. 7:521–551. *figs.* 3. 1909.

[22] COCKAYNE, L., Report on the sand dunes of New Zealand. Department of Lands, Wellington, N.Z. pp. 30. *pls.* 35. 1909.

all species peculiar to New Zealand, but familiar genera such as *Scirpus*, *Festuca*, *Calamagrostis*, and *Euphorbia* are conspicuous. The "sandgrass" dunes and the shrub dunes represent the chief dune plant associations, the almost entire absence of forests being noticeable. A bibliography of the literature relating to the New Zealand dunes completes the interesting report.—GEO. D. FULLER.

Isolated ovulate plants of Mercurialis.—In a recent paper on the determination of sex[23] STRASBURGER described the behavior of isolated ovulate plants of *Mercurialis annua*. The subsequent behavior of these plants is now described.[24] They remained sterile for months, then formed staminate flowers and began to fruit. The pollen of staminate flowers is shed immediately when the anthers dehisce, and the flower drops off the next day, so that they might easily escape observation. Isolated sterile ovulate plants, when pollinated with the pollen of staminate individuals, produce staminate and ovulate plants in about equal numbers; but when pollinated with pollen from the scattered staminate flowers of ovulate plants, the resulting plants are almost exclusively ovulate. When ovulate plants have been pollinated with pollen from a staminate individual and have fruited, they begin to produce scattered staminate flowers. The haploid number of chromosomes, as counted in the pollen mother cells, is 7, and the diploid, both in young embryos and older plants, is 14. There are no adventitious embryos. Both in the observations and in the discussion of the results, this paper adds to STRASBURGER'S already important contributions to the problem of the determination of sex.—CHARLES J. CHAMBERLAIN.

Coastal deserts of Jamaica.—Studying the south coast of Jamaica, SHREVE[25] has explained the desert-like character of an area extending some 70 miles west of Kingston as edaphic areas of desert in a savanna region. The rainfall, 32 inches a year, is capable of supporting a savanna where the soil is deep, the desert being sharply confined to limestone areas with very thin soils and an extremely rough surface. The use of the porous cup atmometer shows an evaporation similar to that of the humid coastal regions in the subtropical United States and much less than that of the inland desert region. The vegetation, however, closely resembles that of the continental desert, being characterized by various species of *Acacia*, *Cassia*, *Cereus*, and *Opuntia*. Bordering the desert there is often a zone of thorn forest, made up almost exclusively of *Prosopis juliflora*. Similar deserts result from similar factors on the coasts of Cuba, San Domingo, and many of the smaller West Indian islands.—GEO. D. FULLER.

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[23] Review in BOT. GAZETTE **48**:63. 1909.

[24] STRASBURGER, E., Das weitere Schicksal meiner isolierten weiblichen *Mercurialis annua*-Pflanzen. Zeitschrift für Botanik **1**:507–524. *pl. 14*. 1909.

[25] SHREVE, FORREST, The coastal deserts of Jamaica. Plant World **13**:129–135. 1910.

Embryos of Angiopteris and Kaulfussia.—In connection with a study of these two genera, CAMPBELL[26] has presented the embryo-formation of Marattiaceae. He thinks it probable that in all cases the stem, leaf, and root are epibasal in origin. In *Danaea* the primary hypobasal cell forms a suspensor, so that the foot also is epibasal; and in *Kaulfussia* and *Angiopteris* the foot is also partly epibasal in origin. The root arises endogenously as a secondary structure, and in its growth almost obliterates the foot, which is very large in the young embryo.—J. M. C.

Anatomy of Calamostachys.—HICKLING[27] has studied new sections of *C. Binneyana*, and has come to the conclusion that the so-called fertile or sporangiophore-bearing "nodes" are not nodes in the same sense as the bract-bearing nodes. He shows that the sporangiophore trace arises from the node that supplies the whorl of bracts below, and he believes this to be a general characteristic of calamitean strobili, the point of insertion of the sporangiophores on the internode being very variable.—J. M. C.

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[26] CAMPBELL, D. H., The embryo and young sporophyte of *Angiopteris* and *Kaulfussia*. Ann. Jard. Bot. Buitenzorg II. Suppl. III. pp. 69–82. *pls. 6, 7.* 1909.

[27] HICKLING, GEORGE, The anatomy of *Calamostachys Binneyana* Schimper. Mem. and Proc. Manchester Lit. and Phil. Soc. **54**:no. 17. pp. 16. *pl. 1.* 1910.

GENERAL INDEX

Classified entries will be found under Contributors and Reviews. New names and names of new genera, species, and varieties are printed in **bold face** type; synonyms in *italic*.

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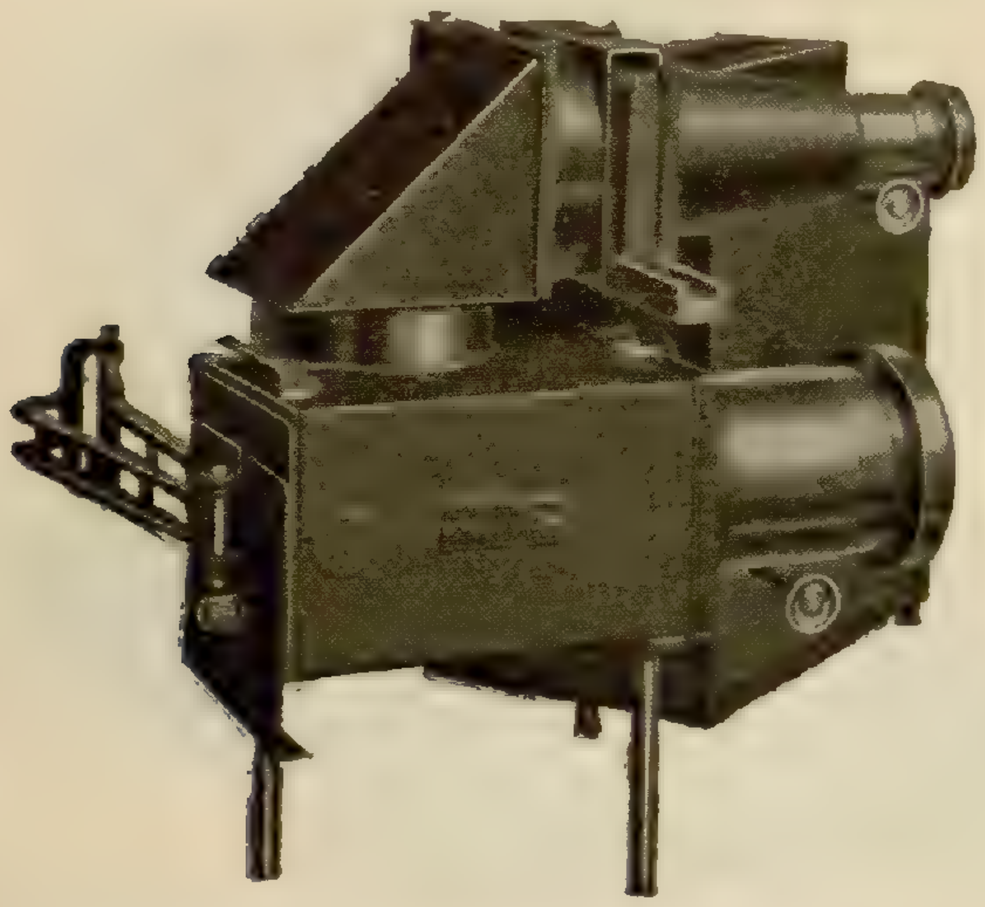

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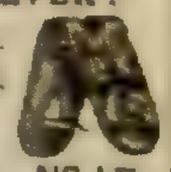

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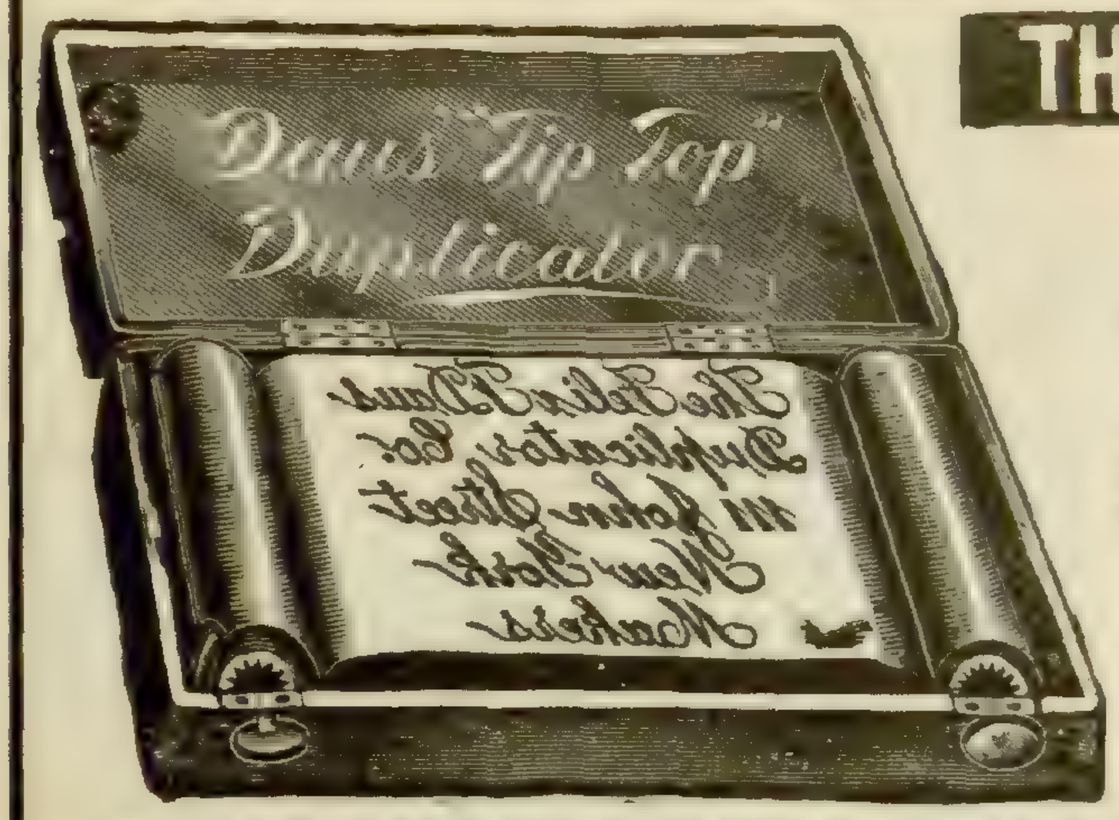

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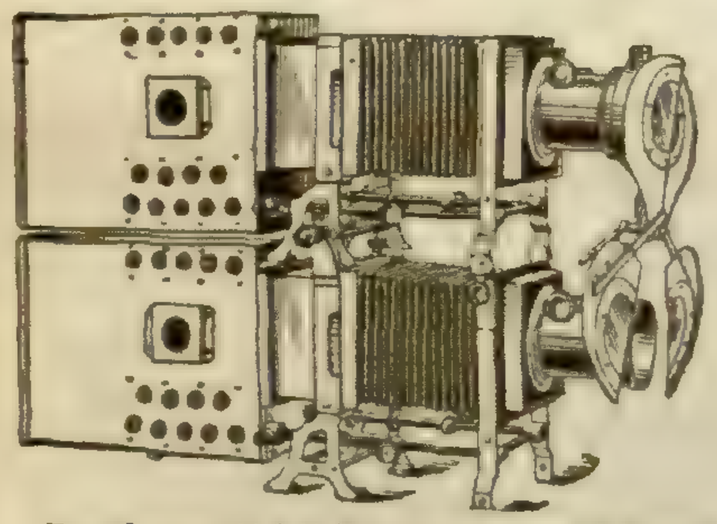

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